

Global Stability in a General Impulsive Biological Control Model with Harvest

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Abstract: In this paper, the effects of periodic partial harvesting of a continuously grown crop on augmentative biological control are analysed. Partial harvesting can remove a proportion of both pests and biological control agents, so its influence on the control efficiency cannot be *a priori* neglected. An impulsive model consisting of a general predator-prey model in ODE is used. It is augmented by a discrete component to depict releases of biological control agents and the periodic partial harvesting. A stability condition for pest eradication is expressed as the minimal value of the budget per unit time to spend on predators. We consider the partial harvesting period to be fixed so that the only manipulated variable is the release period. One period is taken as the integer multiple of the other. We show that when the releases are carried out more often than the harvests, the release period influences the minimal budget. Conversely, there is no effect on this budget when releases take place as often as or less frequently than harvests.

1. INTRODUCTION

Biological control is the reduction of pest populations to harmless levels through the release of their natural enemies. The target pest species and the setting usually determine the type of control required, namely whether pest eradication is necessary or not. For an exhaustive list of definitions and applications, we refer the reader to Eilenberg et al. [2001]. In this paper, we consider the implementation of biological control through natural predators to protect continuously grown crops which have zero tolerance to pest invasions. Examples are flowers of high cosmetic value, as well as fruits and vegetables, which, upon being attacked by a pest, become inedible. There are three aspects in the formulation of this problem:

- Firstly, the most appropriate method of protection in such a case is inundative or augmentative control. This involves a calculated number of predators to be periodically injected into the ecosystem, independently of the detection of pest insects. Such a pre-emptive approach is becoming increasingly popular as it appears to achieve more acceptable pest control (see De Courcy Williams [2001], Jacobson et al. [2001] for real life experiments).
- Secondly, pest eradication is desirable.
- Thirdly, over their growing period, these crops are partially harvested on a regular basis. This practice is likely to remove a proportion of the insects - including the predatory ones - present throughout the plantation. Harvest has already been shown in Volterra [1978] among others to influence, even counterintuitively, predator-prey dynamics. Hence, it is incorporated into the model under study.

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The model consists of ODEs augmented by a discrete component to integrate the effect of partial harvest and releases that by their very nature are discrete phenomena. Few papers in the literature on impulsive crop protection seem to focus on stability of the pest-free state: Liu et al. [2005], Negi and Gakkhar [2007] for instance study the chaotic properties of similar models. Yet this is of practical importance, especially for high valued crop cultures.

We are able to express a stability condition as the minimal number of predators per unit time required to drive the pests to zero. This time unit can be chosen to be the budget year over which the number of predators bought by the grower corresponds to the budget allocated to biological control. In line with the work of Mailleret and Grogard [2006], we investigate how the frequency of releases is to be varied with respect to the (fixed) harvesting frequency to minimise the minimal budget value. We consider the harvest period as the reference since it is set by market constraints and crop dynamics. One period is taken as the integer multiple of the other. This feature is key in solving for the stability condition.

We show that for a given harvest period, when releases take place less often or as often as harvests, the minimal budget is at a calculated value which is independent of release period. However, when releases take place more often than harvests, the minimal budget required always exceeds this value.

In section 2, the system model is described. Next, in section 3, the mathematical analysis of the system's stability and the formulation of the stability condition in terms of the minimal budget are presented. A brief interpretation of the mathematical results follows in section 4. Finally, we conclude with a discussion on their implications.

2. MODEL DESCRIPTION

We consider the case at the onset of pest invasion where the crop - the pest food supply - is in abundance. At this stage, it is sufficient to model a two-dimensional system consisting only of the pest x and predator y species.

$$\begin{cases} \dot{x} = f(x) - g(x)y \\ \dot{y} = h(x)y - dy \\ x(nT_h^+) = (1 - \alpha_x)x(nT_h) \\ y(nT_h^+) = (1 - \alpha_y)y(nT_h) + \delta(nT_h \bmod T_r) \mu T_r \\ y(mT_r^+) = (1 - \delta(mT_r \bmod T_h) \alpha_y)y(mT_r) + \mu T_r \end{cases} \quad (1)$$

$\forall n, m \in \mathbb{N}$ and where $0 \leq \alpha_x, \alpha_y \leq 1$.

Continuous part $f(x)$ is the growth velocity or feeding input of the pests. It represents the growth function of the pest species and in our model, it also encompasses any non-predatory losses of the pest population (e.g. logistic growth). We assume that the predator population is never large enough for intra-predator interaction to take place so the functional and numerical responses can be expressed solely in terms of the prey numbers, i.e. as $g(x)$ and $h(x)$ respectively. The functions discussed are not specified so they are representative of most functions reported in the literature. Only the following hypotheses are made.

Hypothesis 1. Let $f(x)$, $g(x)$ and $h(x)$ be locally Lipschitz continuous in \mathbb{R}^+ such that

- $f(0) = 0$
- $g(0) = 0$, $g'(0) > 0$ and $g(x) > 0 \forall x > 0$
- $h(0) = 0$ and $h(x) > 0 \forall x > 0$
- $\frac{f(x)}{g(x)}$ and $\frac{g(x)}{x}$ are upper bounded for $x \geq 0$

$g(x)$ is increasing for small pest population levels. We also consider that, in the presence of pests, predation always takes place with a negative impact on x ($g(x) > 0$) and a positive impact on y ($h(x) > 0$). In classical density dependent models, $g(x)$ is bounded or linear, so that $\frac{g(x)}{x}$ is always bounded. The boundedness of $\frac{f(x)}{g(x)}$ means that there is no value of x where the pest growth $f(x)$ overwhelmingly dominates the predation $g(x)$, which would render the biological control impossible.

Discrete part Partial crop harvests and predator releases occur respectively every T_h and T_r . α_x and α_y represent the respective proportions of the prey and predator populations affected at each harvest. These parameters are allowed be different since in reality, it is likely that each species occupies different parts of the plant. We also assume that the insects are uniformly distributed throughout our plantation. The $^+$ -superscript denotes the instant right after the relevant impulse is applied. The δ -function is defined thus to identify instants of simultaneous partial harvest and predator release.

$$\delta(\theta) = \begin{cases} 1 & \text{if } \theta = 0 \\ 0 & \text{otherwise} \end{cases}$$

μ refers to the total number of predators purchased per time unit. So as to give an economic dimension to the solution, the time unit will be the budget time period for which a crop grower will invest that number μ . In this same unit, μT_r is the number of predators released every T_r .

3. MATHEMATICAL ANALYSIS

While the formalism in model (1) is more general, we restrict ourselves to the case where either one of the periods (release or partial harvests) is the integer multiple of the other. We study the stability of the system around $x = 0$. In addition of being invariant, it is the target state. Our analysis takes place separately for the case when releases are more frequent than harvests, and when they are less frequent.

3.1 Pest-free stability analysis

Releases more frequent than harvests

Proposition 2. Let $T_h = kT_r$ where $k \in \mathbb{N}^*$ and Hypotheses 1 be satisfied. Then, in the absence of pests, model (1) possesses a globally stable periodic solution $(x_{ph}(t), y_{ph}(t))$ such that

$$\begin{cases} x_{ph}(t) = 0 \\ y_{ph}(t) = y^* e^{-d(t \bmod T_h)} + \mu T_r e^{-d(t \bmod T_r)} \Lambda \end{cases} \quad (2)$$

with $\Lambda = \sum_{j=0}^{\lfloor \frac{t \bmod T_h}{T_r} \rfloor - 1} e^{-jdT_r}$, and where

$$y^* = \frac{\left(\frac{1-e^{-dT_h}}{1-e^{-dT_r}}\right)(1-\alpha_y) + \alpha_y}{1 - (1-\alpha_y)e^{-dT_h}} \mu T_r \quad (3)$$

Proof. When $T_h = kT_r$, in the absence of pests and using Hypotheses 1, the system is simplified to

$$\begin{cases} \dot{x} = 0 \\ \dot{y} = -dy \\ x(mT_r^+) = (1 - \delta(m \bmod k) \alpha_x)x(mT_r) \\ y(mT_r^+) = (1 - \delta(m \bmod k) \alpha_y)y(mT_r) + \mu T_r \\ \forall m \in \mathbb{N} \end{cases}$$

The pest population stays nil since in the absence of pests, their population does not change either. The solution

$$x_{ph}(t) = 0$$

is trivial. On the other hand, the predator population will vary according to the number of predators manually injected into the system and, since the population is non-zero, according to the partial harvest effect. The absence of their source of food will cause an exponential decay of the population. We demonstrate that these forces will provoke the predator population to reach a periodic pattern of period equal to T_h , which we shall refer to as the *period of reference*. The instant following a coinciding partial harvest and release is taken as the *point of reference*.

To prove Proposition 2, we first express the predator population right after a release in terms of the point of reference as

$$y(nT_h + iT_r^+) = y(nT_h^+) e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r} \quad (4)$$

where $i \in [0, 1, \dots, (k-1)]$. This can be verified by induction [Nundloll et al., 2007].

To evaluate the evolution of y according to the period of reference T_h , we need to calculate the value of $y((n+1)T_h^+)$, which is equivalent to $y(nT_h + kT_r^+)$, in terms of $y(nT_h^+)$. At this point however, we suppose

that partial harvesting takes place before predator release so as not to directly waste predators; so we first express it in terms of $y(nT_h + (k-1)T_r^+)$ then expand the expression using (4) as follows

$$\begin{aligned}
 & y((n+1)T_h^+) \\
 &= y(nT_h + (k-1)T_r^+) e^{-dT_r}(1-\alpha_y) + \mu T_r \\
 &= \left(y(nT_h^+) e^{-d(k-1)T_r} + \mu T_r \sum_{j=0}^{k-2} e^{-jdT_r} \right) e^{-dT_r}(1-\alpha_y) \\
 &\quad + \mu T_r \\
 &= y(nT_h^+) e^{-dT_h} + \mu T_r(1-\alpha_y) \sum_{j=1}^{k-1} e^{-jdT_r} + \mu T_r \\
 &= y(nT_h^+) e^{-dT_h} + \mu T_r \left((1-\alpha_y) \sum_{j=0}^{k-1} e^{-jdT_r} + \alpha_y \right)
 \end{aligned} \tag{5}$$

In this linear dynamical system, the coefficient of $y(nT_h^+)$, e^{-dT_h} is less than one in magnitude, so the sequence will converge to a limit, the equilibrium of (5). This equilibrium yields (3) and the convergence of $y(t)$ to a periodic solution $y_{ph}(t)$ based on y^* .

Now that we have established the existence of the periodic solution $y_{ph}(t)$, we seek to formulate it. We focus on a reference period over $nT_h < t \leq (n+1)T_h$ during which $y_{ph}(t)$ is piecewise continuous, with the continuous components separated by predator releases. The continuous intervals are defined over $nT_h + iT_r < t \leq nT_h + (i+1)T_r$ where $i \in [0, 1, \dots, k-1]$. For a given value of t , the value of i is easily identified as being $i = \lfloor \frac{t \bmod T_h}{T_r} \rfloor$. The value of $y_{ph}(t)$ is then of the form

$$y_{ph}(t) = y_{ph}(nT_h + iT_r^+) e^{-d(t \bmod T_r)}$$

and, from (4) with $y(nT_h^+) = y^*$, we have that

$$y_{ph}(nT_h + iT_r^+) = y^* e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r}$$

so that

$$\begin{aligned}
 y_{ph}(t) &= \left(y^* e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r} \right) e^{-d(t \bmod T_r)} \\
 &= y^* e^{-d(t \bmod T_h)} + \mu T_r e^{-d(t \bmod T_r)} \sum_{j=0}^{i-1} e^{-jdT_r}
 \end{aligned}$$

Using the original notation where $i = \lfloor \frac{t \bmod T_h}{T_r} \rfloor$ leads to the same form as proposed in (2), thereby completing our proof.

Releases less frequent than harvests When harvesting is more frequent than the release of predators, we have a similar result about the existence of a periodic solution.

Proposition 3. Let $T_r = kT_h$ where $k \in \mathbb{N}^*$ and Hypotheses 1 be satisfied. Then, in the absence of pests, model (1) possesses a globally stable periodic solution

$$(x_{pr}(t), y_{pr}(t)) = \left(0, y^* e^{-d(t \bmod T_r)} (1-\alpha_y)^{\lfloor \frac{t \bmod T_r}{T_h} \rfloor} \right)$$

where

$$y^* = \frac{\mu T_r}{1 - (1-\alpha_y)^k e^{-dT_r}}$$

The proof is constructed in the same manner as for Proposition 2, and is detailed in [Nundloll et al., 2007].

The form of the y_{ph} and y_{pr} functions is illustrated on Figure 1.

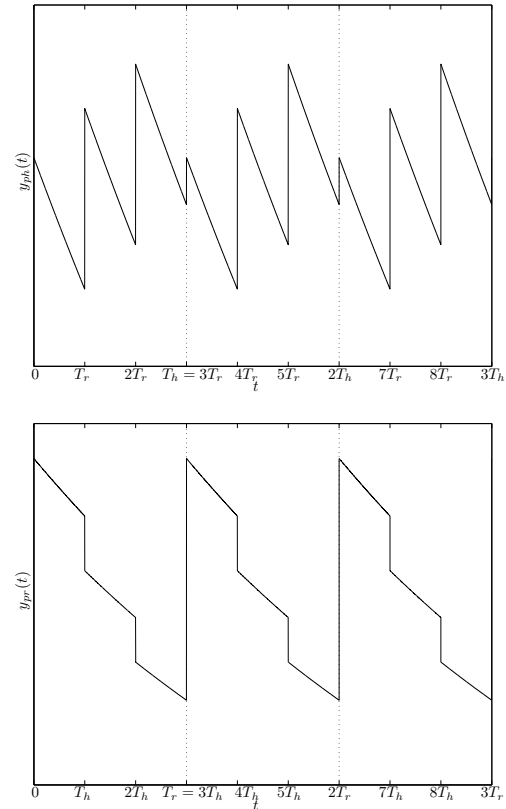


Fig. 1. *Top* Periodic solution $y_{ph}(t)$ in the case where $k = 3$. Releases of predators are apparent at every mT_r instant. *Bottom* Periodic solution $y_{pr}(t)$ in the case where $k = 3$. Harvests are apparent at every nT_h instant, while the release of predators dominates the harvest at every mT_r instant. Between impulses, the population decays exponentially since it has no prey to feed on.

3.2 Stability analysis in the presence of pests

We will now show that, when preys are present at the initial time, convergence of the predator population also takes place at that same periodic solution, while the preys go extinct provided some condition on the parameters is verified.

Since we will study the convergence of the solutions to $(0, y_p(t))$ (where the p subscript stands as well for ph or pr), it will be convenient to describe the system in terms of the deviation coordinates with respect to the reference periodic solution, $(\tilde{x}(t), \tilde{y}(t)) = (x(t) - x_p(t), y(t) - y_p(t))$. This yields

$$\begin{cases} \dot{\tilde{x}} = f(x) - g(x)y = f(\tilde{x}) - g(\tilde{x})(\tilde{y} + y_p(t)) \\ \dot{\tilde{y}} = h(x)y - dy - h(x_p)y_p + dy_p = h(\tilde{x})(\tilde{y} + y_p(t)) - d\tilde{y} \end{cases}$$

The harvest effects on \tilde{x} and for \tilde{y} are obviously unchanged compared to those on x and y . On the other hand, the release effects on y disappear in \tilde{y} ; indeed, we have

$$\begin{aligned} \tilde{y}(mT_r^+) &= y(mT_r^+) - y_p(mT_r^+) \\ &= y(mT_r) + \mu T_r - (y_p(mT_r) + \mu T_r) = \tilde{y}(mT_r) \end{aligned}$$

To perform a global and a local stability analysis, we will also need the computation of the linear approximation of the deviation system around the periodic solution $(0, y_p(t))$:

$$\begin{cases} \dot{\tilde{x}} = (f'(0) - g'(0)y_p(t))\tilde{x} \\ \dot{\tilde{y}} = h'(0)y_p(t)\tilde{x} - d\tilde{y} \end{cases} \quad (6)$$

We obtain two different constraints for the Local Asymptotic Stability (LAS) and Global Asymptotic Stability (GAS) of the periodic solution in system (1). The latter is obviously stronger than the former, but is sufficient in the case where pests outbreaks do not immediately take large proportions.

Releases more frequent than harvests In order to state the following theorem, we first need to define the function

$$\underline{\mu}_h(S, r) = d \left(S + \frac{\ln(1 - \alpha_x)}{rT_h} \right) \frac{1}{1 - \left(\frac{\alpha_y(1 - e^{-dT_h})}{1 - (1 - \alpha_y)e^{-dT_h}} \right) \Gamma}$$

where $\Gamma = \frac{e^{-dT_h/k}}{k(1 - e^{-dT_h/k})}$, and S and r are constants. This function is increasing in S and r because the sign of the partial derivatives is determined by the sign of factor Γ , which is positive [Nundloll et al., 2007].

Theorem 4. When $T_h = kT_r$ with $k \in \mathbb{N}^*$, the solution $(x(t), y(t)) = (0, y_{ph}(t))$ of (1) is LAS iff

$$\mu > \underline{\mu}_h \left(\frac{f'(0)}{g'(0)}, g'(0) \right) \quad (7)$$

and is GAS if

$$\mu > \underline{\mu}_h(S_g, r_g) \quad (8)$$

where $S_g = \sup_{x \geq 0} \frac{f(x)}{g(x)}$ and $r_g = \sup_{x \geq 0} \frac{g(x)}{x}$

Proof. We start with the proof of global convergence under condition (8). In this proof, we will first show that \tilde{x} goes to zero, from which we will derive that \tilde{y} goes to 0 also (so that $y(t)$ converges to $y_{ph}(t)$).

Let the initial condition for system (6) be $(\tilde{x}_0, \tilde{y}_0)$ at time $t_0 = 0^+$, that is after the harvest and the predator release that take place at the initial time. Analysing (6) and noting that $y_{ph}(t) + \tilde{y} = y(t) \geq 0$, we have

$$\dot{\tilde{y}} \geq -d\tilde{y}$$

so that $\tilde{y}(t) \geq \min(0, \tilde{y}_0)e^{-dt}$.

In order to analyse the \tilde{x} equation, we define the function

$$G(\tilde{x}) = \int_{x_0}^{\tilde{x}} \frac{1}{g(s)} ds \quad (9)$$

which can easily be seen to be an increasing function of \tilde{x} since $g(s) > 0$. We also have that $g(s) < \left(\sup_{x \geq 0} \frac{g(x)}{x} \right) s$, therefore $\lim_{\tilde{x} \rightarrow \infty} G(\tilde{x}) = -\infty$. In

order to show the extinction of the pests we will then prove that $G(\tilde{x})$ goes to $-\infty$ as t goes to infinity. We start by writing the G -dynamics:

$$\begin{aligned} \frac{dG(\tilde{x})}{dt} &= \frac{1}{g(\tilde{x})} \dot{\tilde{x}} = \frac{f(\tilde{x})}{g(\tilde{x})} - \tilde{y} - y_{ph}(t) \\ &\leq \frac{f(\tilde{x})}{g(\tilde{x})} - \min(0, \tilde{y}_0)e^{-dt} - y_{ph}(t) \end{aligned}$$

We then consider the evolution of G between two successive harvests, that is between the times nT_h^+ and $(n+1)T_h$ for a given n :

$$\begin{aligned} G(\tilde{x}((n+1)T_h)) &\leq G(\tilde{x}(nT_h^+)) \\ &+ \int_{nT_h^+}^{(n+1)T_h} \left[\frac{f(\tilde{x}(s))}{g(\tilde{x}(s))} - \min(0, \tilde{y}_0)e^{-ds} - y_{ph}(s) \right] ds \end{aligned}$$

Since no impulse is present inside the integral, we can drop the $^+$ superscript in its lower extremity.

We now analyse how the harvest that takes place at time $(n+1)T_h$ impacts G . We have

$$\begin{aligned} G(\tilde{x}((n+1)T_h^+)) &= G(\tilde{x}((n+1)T_h)) + \int_{\tilde{x}((n+1)T_h)}^{\tilde{x}((n+1)T_h^+)} \frac{1}{g(s)} ds \\ &\leq \int_{\tilde{x}((n+1)T_h)}^{\tilde{x}((n+1)T_h^+)} \frac{1}{g(s)} ds + G(\tilde{x}(nT_h^+)) \\ &+ \int_{nT_h}^{(n+1)T_h} \left[\frac{f(\tilde{x}(s))}{g(\tilde{x}(s))} - \min(0, \tilde{y}_0)e^{-ds} - y_{ph}(s) \right] ds \end{aligned} \quad (10)$$

The first term represents the influence of harvest on G and can easily be approximated because $\tilde{x}((n+1)T_h) > \tilde{x}((n+1)T_h^+) = (1 - \alpha_x)\tilde{x}((n+1)T_h)$. Substituting in S_g and r_g , we have

$$\begin{aligned} \int_{\tilde{x}((n+1)T_h)}^{(1-\alpha_x)\tilde{x}((n+1)T_h)} \frac{1}{g(s)} ds &\leq \int_{\tilde{x}((n+1)T_h)}^{(1-\alpha_x)\tilde{x}((n+1)T_h)} \frac{1}{r_g s} ds \\ &= \frac{\ln(1 - \alpha_x)}{r_g} \end{aligned} \quad (11)$$

Introducing (11) into (10) then yields a bound on the application between successive moments after harvest.

$$\begin{aligned} G(\tilde{x}((n+1)T_h^+)) &\leq \frac{\ln(1 - \alpha_x)}{r_g} + G(\tilde{x}(nT_h^+)) \\ &+ \int_{nT_h}^{(n+1)T_h} \left[\frac{f(\tilde{x}(s))}{g(\tilde{x}(s))} - \min(0, \tilde{y}_0)e^{-ds} - y_{ph}(s) \right] ds \end{aligned}$$

We can now evaluate an upper-bound for G at any time $t \geq 0$. Defining l as the integer part of $\frac{t}{T_h}$, we have:

$$\begin{aligned} G(\tilde{x}(t)) - G(x_0) &\leq \int_0^t \left[\frac{f(\tilde{x}(s))}{g(\tilde{x}(s))} - \min(0, \tilde{y}_0)e^{-ds} - y_{ph}(s) \right] ds \\ &+ l \frac{\ln(1 - \alpha_x)}{r_g} \\ &\leq \int_0^t [S_g - \min(0, \tilde{y}_0)e^{-ds} - y_{ph}(s)] ds + l \frac{\ln(1 - \alpha_x)}{r_g} \\ &= - \int_0^t \min(0, \tilde{y}_0)e^{-ds} ds + \int_{lT_h}^t [S_g - y_{ph}(s)] ds \\ &+ l \int_0^{T_h} [S_g - y_{ph}(s)] ds + l \frac{\ln(1 - \alpha_x)}{r_g} \\ &= \frac{\min(0, \tilde{y}_0)}{d} (e^{-dt} - 1) + \int_{lT_h}^t [S_g - y_{ph}(s)] ds \\ &+ l \int_0^{T_h} [S_g - y_{ph}(s)] ds + l \frac{\ln(1 - \alpha_x)}{r_g} \end{aligned}$$

The first two terms are bounded (the first one is obvious and the second one is upper-bounded by $S_g T_h$). We then

have to analyse the third one, which has been obtained through the periodicity of $y_{ph}(t)$ and the fourth in order to know if $G(\tilde{x}(t))$ goes to $-\infty$ when t goes to infinity. In fact, it suffices to have

$$\int_0^{T_h} [S_g - y_{ph}(s)] ds + \frac{\ln(1 - \alpha_x)}{r_g} < 0$$

to achieve this. It is more clearly rewritten in the form

$$\int_0^{T_h} y_{ph}(t) dt > S_g T_h + \frac{\ln(1 - \alpha_x)}{r_g} \quad (12)$$

In order to obtain (8), we are now left with the computation of $\int_0^{T_h} y_{ph}(t) dt$, which is detailed in [Nundloll et al., 2007].

$$\int_0^{T_h} y_{ph}(t) dt = \frac{\mu T_h}{d} \left(1 - \left(\frac{\alpha_y (1 - e^{-dT_h})}{1 - (1 - \alpha_y) e^{-dT_h}} \right) \Gamma \right) \quad (13)$$

Introducing (13) into (12) then yields (8), which shows that this last condition is sufficient for having \tilde{x} going to 0 as t goes to ∞ .

Since \tilde{x} goes to zero, there exists a finite time t_f after which $h(\tilde{x}) \leq \frac{d}{2}$ for all times. Therefore, after this time,

$$\dot{\tilde{y}} = h(\tilde{x})(y_{ph}(t) + \tilde{y}) - d\tilde{y} \leq h(\tilde{x})y_{ph}(t) - \frac{d}{2}\tilde{y}$$

We have seen that $h(\tilde{x})y_{ph}(t)$ goes to zero as t goes to infinity; so does \tilde{y} also.

In order to have the global asymptotic stability, we are only left with the local asymptotic stability to prove. In order to do that, we only have to consider the discrete system that maps the state at time nT_h^+ onto the state at time $(n+1)T_h^+$ with respect to the linear equation (6) and the discrete part [Shulgin et al., 1998]. After some computations, we obtain:

$$\begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} ((n+1)T_h^+) = \mathbf{B} \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} (nT_h^+)$$

where

$$\mathbf{B} = \begin{pmatrix} (1 - \alpha_x)e^{-\int_{nT_h}^{(n+1)T_h} f'(0) - g'(0)y_{ph} d\tau} & 0 \\ \ddagger & (1 - \alpha_y)e^{-d \int_{nT_h}^{(n+1)T_h} d\tau} \end{pmatrix}$$

Since the matrix is triangular, it is stable if $|B_{11}| < 1$, i.e.

$$\int_{nT_h}^{(n+1)T_h} y_{ph} d\tau > \frac{f'(0)T_h + \ln(1 - \alpha_x)}{g'(0)} \quad (14)$$

Similarly to what was done earlier, it can be shown that (14) is equivalent to (7), so that the necessary and sufficient condition for local stability is proven.

It is directly seen that (14) is satisfied when (12) is because $\underline{\mu}_h(S, r)$ is increasing in S and r and we have

$$\begin{aligned} \frac{f'(0)}{g'(0)} &= \lim_{x \gtrsim 0} \frac{f(x)}{g(x)} \leq \sup_{x \geq 0} \frac{f(x)}{g(x)} \\ g'(0) &= \lim_{x \gtrsim 0} \frac{g(x)}{x} \leq \sup_{x \geq 0} \frac{g(x)}{x} \end{aligned}$$

This completes the proof of global stability, since we have shown global convergence and local stability when (8) is satisfied.

Releases less frequent than harvests If we now consider the case where predators releases take place less often than harvests, we also obtain global and local stability results based on the following function

$$\underline{\mu}_r(S, r) = d \left(S + \frac{\ln(1 - \alpha_x)}{rT_h} \right) \frac{1 - (1 - \alpha_y)e^{-dT_h}}{1 - e^{-dT_h}}$$

which is increasing in S and r since the last fraction is positive and $\alpha_x \leq 1$.

Theorem 5. When $T_r = kT_h$ with $k \in \mathbb{N}^*$, the solution $(x(t), y(t)) = (0, y_{pr}(t))$ of (1) is LAS iff

$$\mu > \underline{\mu}_r \left(\frac{f'(0)}{g'(0)}, g'(0) \right) \quad (15)$$

and is GAS if

$$\mu > \underline{\mu}_r \left(\sup_{x \geq 0} \frac{f(x)}{g(x)}, \sup_{x \geq 0} \frac{g(x)}{x} \right)$$

This proof does not depart very much from the one of Theorem 4, and is given in detail in [Nundloll et al., 2007].

Comment As we have seen, when the condition (8) or (5) is satisfied, the extinction of the pests is GAS. When the local condition (7) or (15) is not verified, the extinction of the pests is not stable and a bifurcation analysis similar to what is done in Lakmeche and Arino [2000], Liu et al. [2005] would show the presence of a limit cycle when μ is close to the limit. For smaller values of μ , chaos can arise. When μ satisfies condition (7) or (15) only, the pests extinction is locally stable and we cannot rule out that it is globally stable (since our global condition is only sufficient). Such a budget has the advantage of being smaller than the one that guarantees global stability. It allows for good control of limited pest invasions; however the culture is at risk of being destroyed by a large pest outbreak. We also need to note that when $S + \frac{\ln(1 - \alpha_x)}{rT_h} < 0$, for any of the local or global condition, the condition is trivially verified. Indeed, it implies simply that no biological control is needed for exterminating the pests; in fact, the partial harvesting is effective enough for this purpose (as α_x is large enough).

4. INTERPRETATION OF RESULTS

It is clear from (15) that $\underline{\mu}_r$ is independent of T_r . The latter's influence for non-trivial values of $\underline{\mu}_h$ is formulated in the following theorem,

Theorem 6. Let $T_h = kT_r$ where $k \in \mathbb{N}^*$.

The minimal budget is monotonically decreasing with respect to the release period T_r for non-negative values of $\underline{\mu}_h$, i.e.

$$\frac{\partial \underline{\mu}_h}{\partial T_r} < 0 \quad (16)$$

the proof of which can be found in [Nundloll et al., 2007].

We can deduce that we hit the smallest minimal value for the budget for the largest possible T_r in this case that corresponds to when $k = 1$. This happens when the release frequency equals the partial harvest frequency. Figure 2 represents the analytical results formulated in

the Theorem 6, and obtained from the expressions (7) and (15).

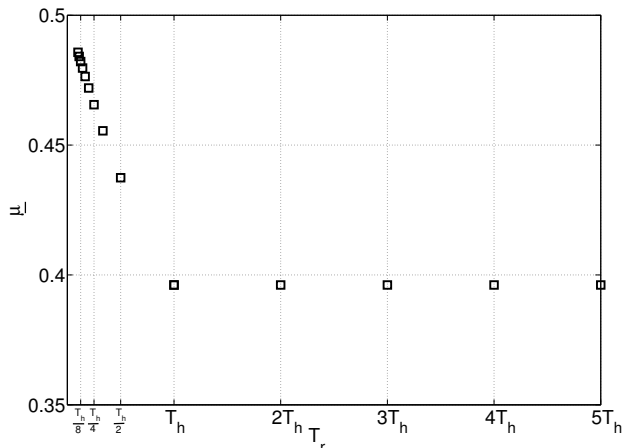


Fig. 2. Variation of the minimal number of predators required per budget year μ as a function of release to harvest period ratio. Parameters are given the values (in arbitrary units): $\alpha_x = \alpha_y = 0.5$, $d = 1$, and the rate of growth $f'(0)$, functional response $g'(0)$ and numerical response $h'(0)$ when the ecosystem is pest-free, i.e. $x_p(t) = 0$, are all equal to 1.

These results imply that it is clearly less costly to protect a greenhouse culture for lower frequencies of release. Of additional economic interest, in this case, the biological treatment is always combined with partial harvesting, so that there is little or no extra cost linked to the presence of workers on-site. However, this result runs counter to that obtained by Mailleret and Groggnard [2006] who demonstrated that the higher the release frequency, the smaller the worst-case damages. Merging the two, for the set of possibilities considered, seems to indicate that the harvest frequency is a threshold that should not be exceeded when releasing predators for efficient biological control.

We are also concerned with the real-life applicability of this result and we are currently working out the design of an experimental setup that would allow us to test our conclusions. Data from a preliminary field test in fact seem to confirm the validity of our theoretical approach.

5. CONCLUSION

Our study was based on the biological control of continuously grown crops which are partially harvested on a regular basis. We formulated the stability condition for the system in terms of the minimal number of predators to inject over a period of time, formalising mathematically the concept of a minimal budget.

We investigated the combined effects of releases and partial harvests on this minimal budget in terms of the relative frequencies of their implementation. We considered the case where these two events occurred at periods such that one was the integer multiple of the other, and with the two events coinciding over the longer period. We found that the harvest frequency provided a threshold for the release

frequency, below which biological control is less costly. (Note that this threshold does not depend on the absolute value of the harvest period in itself.) Combined with the findings of Mailleret and Groggnard [2006], we concluded that for the set of possibilities that was studied, the current 'best' strategy is when release and harvest frequencies are equal.

This approach has, however, its shortcomings. One is that it is not yet generalised to other scenarios where neither period is the integer multiple of the other. It is possible that these intermediate ratios induce other dynamics in the system. Whether they might stabilise it giving even lower minimal budget values or favour chaos remains to be seen.

Nevertheless, we consider that our results already have a practical economic advantage. Indeed, coinciding periods imply little or no additional costs incurred in terms of labour: the task of predator release can be assigned to workers in charge of partial harvesting.

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