

Limit Cycle in a Herbivore-Plant-Bee Model Containing a Time Delay

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ABSTRACT: The dynamical behavior of time delay herbivore-plant-pollinator ecosystem is studied. The time delay arises from the fact that it takes time for a pollinated flower to develop into a new plant. A dynamical analysis is used to show that a stable steady state undergoes a Hopf bifurcation to a limit cycle behavior as the delay time crosses a critical value. This prediction is verified by numerically solving the set of first order differential equations. One finds that the trajectory which is spiraling into the steady state point when $\tau < \tau_c$ becomes a trajectory into a limit cycle about the state when $\tau > \tau_c$.

KEYWORDS: Herbivore-plant-pollinator ecosystem, time delay, Hopf Bifurcation.

INTRODUCTION

Very recently, Bandyopadhyay, Bhattacharyya and Mukopadhyay (BBM)¹, studied the dynamics of an autotroph-herbivore ecosystem with nutrient recycling. They considered both the case where there is no time delay and the case where there is a delay. For the former case, they found that when the rate of increase of the nutrients attained a certain threshold value, the system became stable. The autotroph and herbivore populations would oscillate about an interior steady state point. Below the threshold value, the system became unstable. Note that in the absence of nutrient replenishing, the nutrients would eventually disappear from the soil and the autotrophic state would go to zero. For the latter case, BBM found that a sufficiently large delay in the time needed to convert dead organic matter into the nutrients, would cause the stable state to become unstable. Using Hopf Bifurcation analysis², they established the conditions for the switching of the stability.

Jang³ has studied the dynamics of a herbivore-plant-pollinator ecosystem. Jang's model is somewhat different from that of BBM. He looked at the roles of the energetic rewards of the interactions between the plant and the pollinator and of the specificity of the pollinator to the plant. Jang was particularly interested in how the reduction of the visitation rate of the bee to the plant caused by the action of the herbivore affected

the ecosystem. A Hopf Bifurcation analysis was again used to determine the stability of the steady states. Jang did not include any time delay^{4,5} into his model.

The purpose of the present paper is to determine the effects of a time delay in Jang's model. Unlike the BBM model, where the time delay should be inserted is obvious, it is not in Jang's model. We believe that it should be inserted into the term describing the birth rate of the plant;

$$\frac{k_1 \sigma \mu XY}{1 + \sigma \phi \mu^2 Y} \quad (1)$$

where X and Y are the bee and plant populations, respectively; k_1 , number of ovules fertilized per visit of the bee; σ , the probability of an encounter between the flower and the bee; ϕ , reciprocal of the time it takes the bee to extract the nectar (or pollen); and μ , the energetic reward to the bee when it encounters the flower. This gives the number of flowers fertilized at time t. It then takes time for the fertilized ovules to develop into seeds and fall to the ground. The number of new plants that will begin to flower at time t will depend on the number of ovules that were fertilized at time $t - \tau$, where τ is the time delay. In Section II, we introduce the Jang model and present some of his results. We put the time delay into the model in Section III, and carry out a Hopf Bifurcation analysis. In Section IV, we present our

numerical solution. In Section V, we present an extension of our model and discuss how it can be used to provide quantitative predictions for the farmers.

II. Jang's Model.

The herbivore-plant-pollinator ecosystem considered by Jang consists of three first order differential equations;

$$\dot{X} = bX(K - X) + \frac{g(Z)k_2\sigma\mu^2XY}{1 + \phi\sigma\mu^2Y} \quad (2a)$$

$$\dot{Y} = \frac{k_1\sigma\mu g(Z)XY}{1 + \phi\sigma\mu^2Y} - \gamma Y - \frac{m_1YZ}{a + Y} \quad (2b)$$

$$\text{and } \dot{Z} = \frac{m_2YZ}{a + Y} - \delta Z \quad (2c)$$

where Z denotes the herbivore population; $g(z)$ represents the loss in attractiveness of the flower to the bee due to the damage caused by the herbivore;

$$\frac{m_2Y}{a + Y} \quad (3)$$

is the visitation rate of the herbivore to the plant; m_1 and m_2 , the maximal ingestion rate and the leafhopper maximal growth rate with $0 < m_2 \leq m_1$, respectively; 'a', the half - saturation constant; δ_1 , the maximum per capita birth rate of the bees; λ and δ , the death rate of the bees and herbivore, respectively; 'b', the density dependent regulation constant of bee, and K is the measure of the diversity of bee to the plant ($K = (\delta_1 - \lambda)/b$). In the present model, the flower on the plant becomes pollinated and after awhile, the plant dies. The life cycle begins again when the seed developed from the pollinated flower falls off the plant and germinates in the soil. All of the population classes must be positive at all times, i.e.,

$$X(t), Y(t), Z(t) \geq 0.$$

Setting the RHS of eqns. (2a)–(2c) to zero, we obtained

$$m_1, \quad \bar{x} = K + \frac{g(\bar{z})k_2\mu^2\sigma\bar{y}}{b(1 + \phi\sigma\mu^2\bar{y})} \quad (4a)$$

$$\bar{y} = \frac{a\delta}{m_2 - \delta}, m_2 > \delta \quad (4b)$$

and

$$\bar{z} = \frac{a + \bar{y}}{m_1} \left[\frac{k_1 k_2 \mu^3 \sigma^2 \bar{y}}{b(1 + \phi\sigma\mu^2\bar{y})^2} g(\bar{z})^2 + \frac{k_1 \mu \sigma K}{1 + \phi\sigma\mu^2\bar{y}} g(\bar{z}) - \gamma \right] \quad (4c)$$

at one of the steady states $(\bar{x}, \bar{y}, \bar{z})$. To determine when the state is stable or not, we first diagonalize the Jacobian of eqns. (2a) to (2c) at the steady state. We then check to see if all the eigenvalues have negative real parts. When this happens, the state is stable. Diagonalizing the Jacobian, we obtain the following characteristic equation

$$\lambda^3 + (p_1 - s_1)\lambda^2 + (p_2 - s_2)\lambda + (p_3 - s_3) = 0 \quad (5)$$

where

$$p_1 = \gamma + \delta - bK + 2b\bar{x} - m_2 h(\bar{y}) - k_2 \mu f(\bar{y}) g(\bar{z}) + m_1 \bar{z} h'(\bar{y}),$$

$$p_2 = \gamma\delta - bK\delta - bKy + 2b\bar{y}\bar{x} + bKh(\bar{y})m_2 - \gamma h(\bar{y})m_2 - 2bh(\bar{y})\bar{x}m_2$$

$$+ 2b\delta\bar{x} - \gamma f(\bar{y})k_2\mu g(\bar{z}) - \delta f(\bar{y})k_2\mu g(\bar{z}) + f(\bar{y})h(\bar{y})k_2m_2\mu g(\bar{z})$$

$$- bK\bar{z}m_1h'(\bar{y}) + \delta\bar{z}m_1h'(\bar{y}) + 2b\bar{x}\bar{z}m_1h'(\bar{y}) - f(\bar{y})\bar{z}k_2m_1\mu g(\bar{z})h'(\bar{y}),$$

$$p_3 = 2b\gamma\delta\bar{x} - bK\gamma\delta + bK\gamma h(\bar{y})m_2 - 2b\gamma h(\bar{y})\bar{x}m_2 - \gamma\delta h(\bar{y})k_2\mu g(\bar{z})$$

$$+ \gamma f(\bar{y})h(\bar{y})k_2m_2\mu g(\bar{z}) - bK\delta\bar{z}m_1h'(\bar{y}) + 2b\delta \frac{\bar{x}}{\bar{x}\bar{z}m_1h'(\bar{y})}$$

$$- \delta f(\bar{y})\bar{z}k_2m_1\mu g(\bar{z})h'(\bar{y}),$$

$$s_1 = g(\bar{z})\bar{x} k_1 f'(\bar{y}),$$

$$s_2 = -bKg(\bar{z})\bar{x}k_1 f'(\bar{y}) + \delta g(\bar{z})\bar{x} k_1 f'(\bar{y}) + 2bg(\bar{z})\bar{x}^2 k_1 f'(\bar{y})$$

$$- g(\bar{z})h(\bar{y})\bar{x} k_1 m_2 f'(\bar{y}) + f(\bar{y})\bar{x} \bar{z} k_1 m_2 g'(\bar{z})h'(\bar{y})$$

and

$$s_3 = 2b\delta g(\bar{z})\bar{x}^2 k_1 f'(\bar{y}) - bK\delta g(\bar{z})\bar{x}k_1 f'(\bar{y}) + 2b f(\bar{y})\bar{x}^2 \bar{z} k_1 m_2 g(\bar{z}) h'(\bar{y})$$

$$+ bK g(\bar{z}) h(\bar{y}) \bar{x} k_1 m_2 f(\bar{y}) - 2b g(\bar{z}) h(\bar{y}) \bar{x}^2 k_1 m_2 f(\bar{y})$$

$$- bK f(\bar{y}) \bar{x} \bar{z} k_1 m_2 g'(\bar{z}) h'(\bar{y}) \quad (6)$$

Equation (5) has negative real roots if and only if (Theorem 1, Appendix)

$$P_1 - S_1 > 0, P_3 - S_3 > 0 \text{ and } (P_1 - S_1)(P_2 - S_2) - (P_3 - S_3) > 0. \quad (7)$$

When the above conditions are satisfied $(\bar{x}, \bar{y}, \bar{z})$, the steady state will be stable.

III. Effect of Time Delay.

IIIa. The Stability of $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ with Time Delay.

A time delay in the herbivore-plant-pollinator system arises because a new flower only arrives after the pollinated flower develops into a seed, falls off the plant, germinates into a new plant and then grows into the flowering stage of the new plant. To include the effects of the time delay, we need to replace eqn. (2b) by

$$y = \frac{k_1 \mu \sigma g(z(t - \tau))x(t - \tau)y(t - \tau)}{1 + \phi\sigma\mu^2y(t - \tau)} \quad \gamma y \frac{m_1 y z}{a + y} \quad (2b')$$

The Jacobian matrix for eqns. (2a), (2b') and 2c evaluated at the steady state point $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ is

$$\begin{pmatrix} bK - 2b\bar{x} + k_2 \mu g(\bar{z}) f(\bar{y}) & k_2 \mu g(\bar{z}) f'(\bar{y}) \bar{x} \\ k_1 g(\bar{z}) f(\bar{y}) e^{-\omega\tau} & -\gamma - m_1 \bar{z} h'(\bar{y}) + k_1 g(\bar{z}) \bar{x} f'(\bar{y}) e^{-\omega\tau} \\ 0 & m_2 \bar{z} h'(\bar{y}) \end{pmatrix} \quad (8)$$

Diagonalizing the above matrix, we obtain the following characteristic equation⁵

$$\omega^3 + p_1\omega^2 + p_2\omega + p_3 = e^{-\omega\tau}(s_1\omega^2 + s_2\omega + s_3) \quad (9)$$

We now suppose that two of the eigenvalues of eqn. (9) are a pair of complex conjugates

i.e., $\omega_{\pm} = u(\tau) \pm iv(\tau)$. Substituting ω_{\pm} into eqn. (9) and separating the real and imaginary parts, we get

$$\begin{aligned} & u^3 - 3uv^2 + p_1u^2 - p_1v^2 + p_2u + p_3 \\ &= e^{-\omega\tau}(s_1u^2\cos(v\tau) - s_1v^2\cos(v\tau) + s_2u\cos(v\tau) + s_3\cos(v\tau)) \\ &\quad + 2s_1uv\sin(v\tau) + s_2v\sin(v\tau) \end{aligned} \quad (10)$$

and

$$\begin{aligned} & 3u^2v - v^3 + 2p_1uv + p_2v \\ &= e^{-\omega\tau}\{2s_1uv\cos(v\tau) + s_2v\cos(v\tau) - s_1u^2\sin(v\tau) \\ &\quad + s_1v^2\sin(v\tau) - s_2u\sin(v\tau) - s_3\sin(v\tau)\} \end{aligned} \quad (11)$$

where τ is chosen to be the Hopf bifurcation parameter.

For a Hopf bifurcation to occur, three conditions must be met at the critical value (τ_c): (1) $u(\tau_c) = 0$, (2) $v(\tau_c) \neq 0$ and (3) $u'(\tau_c) > 0$ (Theorem 2, Appendix). To see if the eigenvalues of the Jacobian evaluated at the steady state point $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ satisfy these conditions, we first assume that the critical value defined by $u(\tau_c) = 0$ exist. However, we do not use this condition to find τ_c . Instead we substitute the condition into eqns. (10) and (11) and see whether a non-zero value of $v(\tau_c)$ exist.⁶ To do this, we set $u(\tau_c) = u^* = 0$ into the two equations to get

$$-p_1v^{*2} + p_3 = (s_3 - s_1v^{*2})\cos(v^*\tau_c) + s_2v^*\sin(v^*\tau_c) \quad (12)$$

$$-v^{*3} + p_2v^* = s_2v^*\cos(v^*\tau_c) - (s_3 - s_1v^{*2})\sin(v^*\tau_c) \quad (13)$$

Squaring the two equations and adding the squares together, we obtain

$$\begin{aligned} & v^{*6} + (p_1^2 - 2p_2 - s_1^2)v^{*4} + (p_2^2 - 2p_1p_3 - s_2^2 + 2s_1s_3)v^{*2} + (p_3^2 - s_3^2) = 0 \\ & \quad (14) \end{aligned}$$

Letting $v^{*2} = \eta$ eqn. (14) becomes the following cubic equation

$$S(\eta) = \eta^3 + d_1\eta^2 + d_2\eta + d_3 = 0 \quad (15)$$

where

$$d_1 = p_1^2 - 2p_2 - s_1^2 \quad (16a)$$

$$d_2 = p_2^2 - 2p_1p_3 - s_2^2 + 2s_1s_3 \quad (16b)$$

$$d_3 = p_3^2 - s_3^2 \quad (16c)$$

For $v(\tau_c)$ to exist, the roots of eqn. (15) must be real and

positive. This can be determined by using the results of the lemma stated in the Appendix. We now assume that a set of values for the parameters can be found which satisfies the conditions of Lemma 1.

Next we need to show that for the present $u(\tau)$, the following is true

$$\left. \frac{du}{d\tau} \right|_{\tau=\tau_0} > 0 \quad (17)$$

This is done by differentiating eqns. (10) and (11) with respect to τ and then set $\tau = \tau_c$. Doing this, we get

$$B \left. \frac{du}{d\tau} \right|_{\tau=\tau_0} + C \left. \frac{dv}{d\tau} \right|_{\tau=\tau_0} = D \quad (18a)$$

$$-C \left. \frac{du}{d\tau} \right|_{\tau=\tau_0} + B \left. \frac{dv}{d\tau} \right|_{\tau=\tau_0} = E \quad (18b)$$

where

$$B = \left[-3v_0^2 + p_2 - s_2\cos(v_0\tau_0) - 2s_1v_0\sin(v_0\tau_0) + s_3\tau_0\cos(v_0\tau_0) - s_1v_0^2\tau_0\cos(v_0\tau_0) + s_2v_0\tau_0\sin(v_0\tau_0) \right]$$

$$C = \left[-2p_1v_0 + 2s_1v_0\cos(v_0\tau_0) + s_3\tau_0\sin(v_0\tau_0) - s_1v_0^2\tau_0\sin(v_0\tau_0) - s_2\sin(v_0\tau_0) - s_2v_0\tau_0\cos(v_0\tau_0) \right]$$

$$D = (s_1v_0^3 - s_3v_0)\sin(v_0\tau_0) + s_2v_0^2\cos(v_0\tau_0) \quad \text{and}$$

$$E = (s_1v_0^3 - s_3v_0)\cos(v_0\tau_0) - s_2v_0^2\sin(v_0\tau_0) \quad (19)$$

Solving for $\left. \frac{du}{d\tau} \right|_{\tau=\tau_0}$ we get

$$\left. \frac{du}{d\tau} \right|_{\tau=\tau_0} = \frac{BD - EC}{B^2 + C^2} \quad (20)$$

where

$$BD - EC = v_0^2[3v_0^4 + 2v_0^2(p_1^2 - 2p_2 - s_1^2) + (p_2^2 - 2p_1p_3 - s_2^2 + 2s_1s_3)] \quad (21)$$

Therefore, we have

$$\left. \frac{du}{d\tau} \right|_{\tau=\tau_0} = \frac{v_0^2}{B^2 + C^2}[3v_0^4 + 2v_0^2(p_1^2 - 2p_2 - s_1^2) + (p_2^2 - 2p_1p_3 - s_2^2 + 2s_1s_3)] \quad (22)$$

Noting that

$$\frac{dS}{d\eta} = 3\eta^2 + 2(p_1^2 - 2p_2 - s_1^2)\eta + (p_2^2 - 2p_1p_3 - s_2^2 + 2s_1s_3) \quad (23)$$

where S is defined by eqn. (15), eqn. (22) can be written as

$$\frac{du}{d\tau} \Big|_{\tau=\tau_0} = \frac{v_0^2}{B^2 + C^2} \frac{ds}{d\eta} \Big|_{\eta=v_0^2} . \quad (24)$$

The condition $\Delta < 0$ in part A of Lemma I requires the two turning points of $S(\eta)$ not be a positive real root of $S(\eta)$, otherwise Δ would be equal to zero. The two turning points of $S(\eta), \varepsilon_1$ and ε_2 (eqn. A2), are the zeros of eqn. (23). Since $v_0^2 \neq \varepsilon_{1,2}$, the following must be true

$$\frac{ds}{d\eta} \Big|_{\eta=v_0^2} \neq 0 \quad (25)$$

Thus

$$\frac{du}{d\tau} \Big|_{\tau=\tau_0} = \frac{v_0^2}{B^2 + C^2} \frac{ds}{d\eta} \Big|_{\eta=v_0^2} \quad (26)$$

and condition 3 of the Hopf bifurcation theory is satisfied. Therefore the system undergoes a Hopf bifurcation.

IIIb. Critical Time Delay.

The critical delay time can be found by using the method introduced by Tam.⁶ We rewrite eqns (12) and (13) as

$$M\cos(v * \tau_0) + N\sin(v * \tau_0) = P \quad (27a)$$

$$N\cos(v * \tau_0) - M\sin(v * \tau_0) = Q \quad (27b)$$

where

$$M = S_3 - S_1 V^2 , \quad (28a)$$

$$N = S_2 V^* \quad (28b)$$

$$P = -P_1 V^2 + P_3 \quad (28c)$$

and

$$Q = -V^{*3} + P_2 V^* \quad (28d)$$

Eqns. (27a) and (27b) leads to

$$M^2 + N^2 = P^2 + Q^2 = G^2 , \text{ where } G > 0. \quad (29)$$

M and N can be rewritten as

$$\begin{aligned} M &= G \cos \theta \\ N &= G \sin \theta \end{aligned} \quad (30)$$

This allows us to determine a $\theta \in [0, 2\pi]$ uniquely. With this value of θ , eqns. (27a) and (28b) become

$$G\cos(\tau_0 v^*)\cos\theta + G\sin(\tau_0 v^*)\sin\theta = P \quad (31)$$

$$G\cos(\tau_0 v^*)\sin\theta - G\sin(\tau_0 v^*)\cos\theta = Q \quad (32)$$

or

$$G\cos(\tau_0 v^* - \theta) = P \quad (33a)$$

$$G\sin(\tau_0 v^* - \theta) = Q \quad (33b)$$

From this we get as the critical value

$$\tau_0 = \frac{1}{v^*} \left\{ \tan^{-1} \left(\frac{Q}{P} \right) + \theta \right\} \quad (34)$$

IV. Numerical Solution.

IVa. Numerical Parameters.

The numerical values of the parameters in the herbivore-plant-pollinator ecosystem for a given plant are scarce. One has to guess at them since many of them will depend on which plant we are interested in, what is the locality (or country) or what time of the year it is. To gain ideas of the range of values the parameters can take, we look at the Mango tree, even though the present model is not an appropriate model for this plant. The model is developed for a flowering plant which after becoming pollinated, dies. Most Mango trees exhibit biannual flowering, once between May and June and again in December-January. This flowering is repeated every year for many years. Nevertheless, we have used the data available for the Mango trees to be typical of most plants.

Jamjanya⁷ has looked at the increase in leafhopper population in two varieties of mango trees, On-sorn and Na thub. He found that leafhopper infestation on the Na-thub mango tree increased by 270% in a day, while the leafhoppers infestation on the On-sorn mango tree increased 63% in a day. This implies that m_2 can vary between 0.63 - 2.7 day⁻¹ depending on the type of Mango tree. Boongird⁸ has measured the probability that a bee will visit a Nam dok mai mango tree in Thailand. He found σ to be 79.55%. In Trinidad, the probability that a bee will visit the mango is about 21%.⁹ We take σ , the probability of encounter to be in the range 0.21 - 1.0. The extraction rate of the nectar by the bee range between 0.3 $\mu\text{l/sec}$ in grove and 2.0 $\mu\text{l/sec}$ in pool.¹⁰ ϕ , which is reciprocally related to the speed of nectar extraction, is set to be in the range 1.93×10^{-5} - 3.86×10^{-5} ($\mu\text{l/day}$)⁻¹. Other studies find that a bee will visit 8 - 10 flowers per visit.¹¹ Since only about 5 - 75 % of the flowers are perfect, the number of ovules fertilized per visit, k_1 , will be in the range of 0.4 - 7.5 flowers per visit.

The normal death rate of the bees has been changing. The French National Bee Surveillance Unit¹² has stated that the death of the bees during the winter months was one out of ten in previous years. Now, the death rate is six out of ten. This means that λ is in the range 0.001 - 0.006. For the birth rate of the bees, δ_1 , we assume that the queen bee lays about 1200 - 2000 eggs/day. For a typical small hive containing perhaps 20,000 bees,^{9,13} the birth rate of the bees would be in the range, 0.06 - 0.1 day⁻¹. The estimated values of the parameters are listed in Table I.

IVb. Numerical Solutions.

For the purpose of getting an idea of what might occur, we have set the values of the parameters at: $a = 500$, $b = 1/8$, $\lambda = 0.0035$, $k_1 = 3.95$, $k_2 = 0.00005$, $m_1 = 7.5$, $m_2 = 1.6$, $\phi = 0.0000386$, $\sigma = 0.25$, $\gamma = 0.0111$, $\mu = 23$ and $\delta = 0.05$. Substituting the above values into eqns. (4a)-(4c), we get the steady state

Table 1. Parameter values

Parameters	Units	parameter range
a	no. of flower	500
b	1/(bee day)	1/8
K	no. of bee	$\frac{d_1 - \lambda}{b}$
k_1	mango/(bee visit)	0.4 - 7.5
μ	microliter/visit	22.72-63.63
ϕ	(microliter/day) ⁻¹	$1.93 \times 10^{-5} - 3.86 \times 10^{-5}$
σ	-	0.21 - 1.0
d_1	day ⁻¹	0.06 - 0.1
λ	day ⁻¹	0.001 - 0.006
k_2	microliter ⁻¹	$>1.48 \times 10^{-6}$
γ	day ⁻¹	0.0111
m_1	mango/day	10.93-910.75
m_2	day ⁻¹	0.63 - 2.7
δ	day ⁻¹	0.01-0.05

$$\bar{E}(0.637873, 16.129, 29.4689). \quad (35)$$

Substituting the values of $(\bar{x}, \bar{y}, \bar{z})$ given by eqns. (4a)-(4c) and the values of the parameters into eqn. (7), we find that the Routh-Hurwitz conditions are met and the steady state is stable. Substituting the same values in eqn. (34), we find that the critical value is

$$\tau_c = 1.13 \text{ days} \quad (36)$$

As τ crosses this value, the steady state should become unstable. To see if this happens, we have solved eqns. (2a), (2b') and (2c) (for a delay time of 1 day) using the values of the parameters given above. In Figure 1, we see the trajectory of the solution spiral into the equilibrium state, eqn. (35). This would be expected since $\tau < \tau_c$. We then changed the value of the time delay to be 1.13 days. The trajectory is now a limit cycle (See Figure 2). As we have pointed out, the conditions for the system to undergo a Hopf bifurcation to a limit cycle are met with the values of the parameters used. Finally, we pick $\tau = 10$ days. In Figure 3, we see the trajectory spiraling away from the steady state $\bar{E}(0.637873, 16.129, 29.4689)$. The trajectory initially starts at the left face of the cube, heads towards the steady state and then spirals away from the steady state. This implies that the steady state has become unstable.

To understand why this happens, let us look at the biology. A nonzero steady state with $\bar{y} \neq 0$ would be possible if a new plant would begin to flower while some of the original flowers are still present. This would require that a flower, pollinated at the beginning of the flowering season, would quickly develop into a seed. The seed must then fall to the ground and germinate into a plant that develops new flowers before the original flowers dry up and die. This does not usually happen in nature. Each step in the developmental stage of the plant takes time. Since the new plants do not usually arrive until the next year, the delay time appearing in eqn. (2b') would be one year. Between the period the time the last flowers of the season die and the new ones arrive, there would be no flowering plants present.

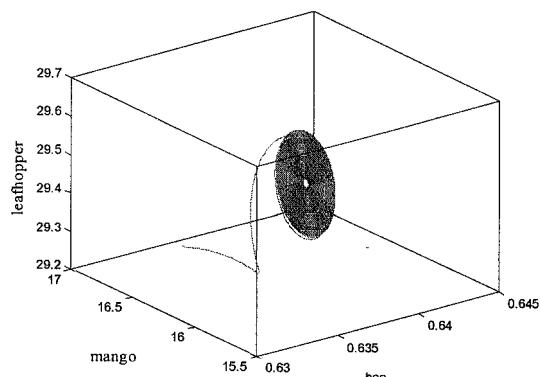


Fig 1. Numerical solution of equations (2a), (2b') and (2c) for a time delay of $t = 1$ ($t < t_c$). The graph shows the trajectory in the 3-D phase plane. The motion spirals toward the steady state solution $\bar{E}(0.637873, 16.129, 29.4689)$. The parameters used are: $a=500$, $b=1/8$, $d_1=0.08$, $l=0.0035$, $k_1=3.95$, $k_2=0.00005$, $m_1=7.5$, $m_2=1.6$, $j=0.0000386$, $s=0.25$, $g=0.0111$, $m=23$, $d=0.05$

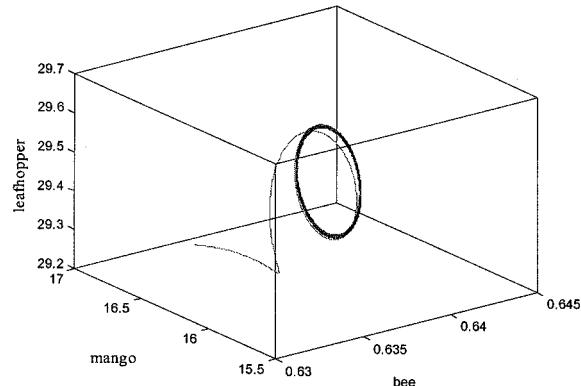


Fig 2. Numerical solution of equations (2a), (2b') and (2c) at the critical time delay $t_c = 1.13$ days. The parameters used are: the same as used for Figures 1. The trajectory projected on 3-dimensional phase plane. The motion is a limit cycle.

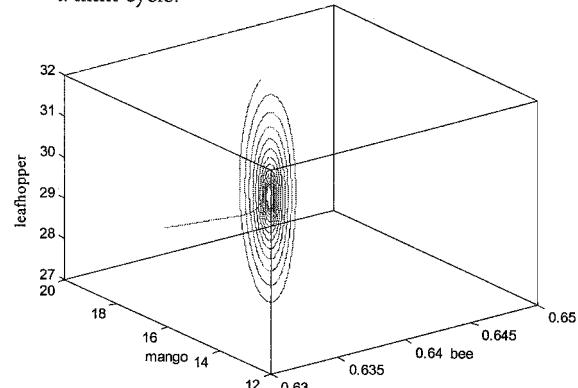


Fig 3. Numerical solution of equations (2a), (2b') and (2c) for a time delay of $t=10$ ($t > t_c$) days. The graph shows the trajectory in the 3-D phase plane. The trajectory moves away from the steady state solution. The parameters used are the same as those used to obtain Figs. 1 and 2.

This would happen if the time delays are greater than the lifetime of the flower, which we have taken to be nine days.

IVc. Real Applications.

To see how the present model might be of use to the farmers, we have modified the model to more accurately describe the production of mangoes. We have inserted into eqn. (2b'), the added term $\Phi\delta(t-t_0)$ to represent the appearance of non pollinated flowers on the tree at time t_0 . Φ is the number of flowers that appear on day t_0 . We have assumed that the time delay is six months which is greater than the critical delay time. Therefore there will be no contribution from the term given by eqn. (1) in eqn. (2b'). We now look to see what would happen if the farmer has more bees on his farm. To see this, we have solved eqns. (2a), (2b') and (2c) using K values of 1000, 1,500 and 2000. The values of the other parameters are given on the figure captions. In Figure 4, we plot the number of flowers on a single tree that get pollinated each day after day t_0 , the day the flowers began to bloom. The initial conditions for the starting day of the computer simulation, are $Y(0)=0$, and $X(0)$ and $Y(0)$ are arbitrary. As the time passes, the number of bees begins to increase until it reaches the saturation value K . On the 100th, the flowers bloom. The figure shows that only for a short period do pollinated flowers get produced. The reason for this is that only during these nine days are the non pollinated flowers present. After this period, the flowers dried up and died. This leads to $y=0$. We also see that the number of flowers that get pollinated increases as the number of bee increases. The three plots provide a quantitative measure of how much more mangoes can be obtained by increasing the number of bees

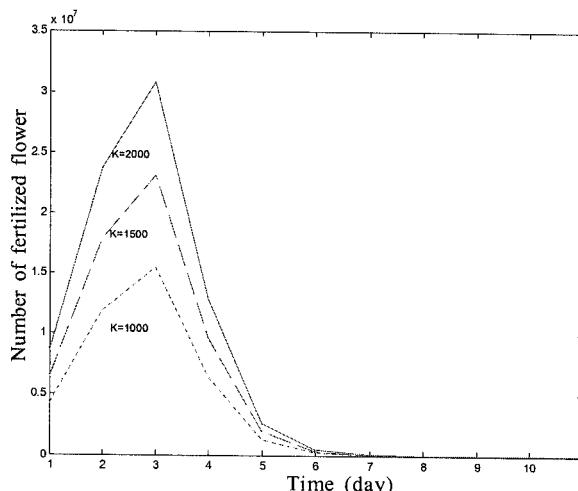


Fig 4. Number of flowers pollinated per day per tree for K equal to 1,000, 1,500 and 2,000. The number of flowers appearing on day t_0 is $F=10,500,000$. The values of the other parameters are the same as used to obtain figs. 1, 2 and 3.

available.

Another practice that can be carried out by the farmer is to decrease the number of leafhoppers. Spraying insecticides or introducing biological pests of the leafhoppers to kill them would accomplish this. The first method would however also decrease the number of bees unless the insecticide is of a type that only affects the leafhoppers and not the bees. We simulate the effects of employing an insecticide of this type or using the second method by increasing the value of the leafhopper's death rate. We have solved eqns. (2a), (2b') and (2c) for three values of the death rate δ (0.05, 0.07 and 0.09). In Figure 5, we see that more flowers would be pollinated if the life time (inversely proportional to the death rate) of the leafhopper were shorten. The time axis is changed so that it starts at day 100. We see that the flowers are only pollinated over a nine day period (i.e., during the period

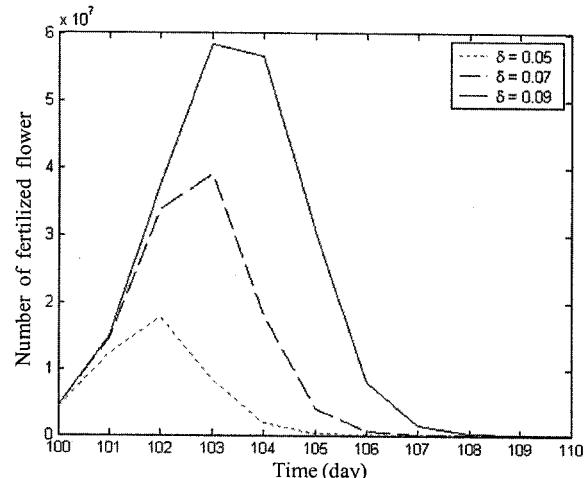


Fig 5. A graph shows the number of fertilized flower per day per tree for the death rate of leafhopper, d , equal to 0.05, 0.07 and 0.09. The number of flowers appearing on day t_0 is $F=10,500,000$. The values of the parameters are: $a=500$, $d_1=0.08$, $l=0.0035$, $k_1=3.95$, $k_2=0.00005$, $m_1=7.5$, $m_2=1.6$, $f=0.0000386$, $s=0.25$, $g=0.0111$, $m=23$, $b=d_1-l$, $K=1000$

the flowers are present on the tree).

Another way for the number of pollinated flowers to be increased is to increase the number of flowers on the tree. This could be done by having the rain arrive at the right time and/or having a new variety of mango plants that have more flowers. These are however beyond the control of the farmer.

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APPENDIX

Lemma 1. Conditions for the Existence of Positive Real Roots of a Cubic Equation.

Consider the following cubic equation

$$S(\eta) = \eta^3 + d_1\eta^2 + d_2\eta + d_3 = 0 \quad (A1)$$

A. If either (i) $d_1 < 0$, $d_2 \geq 0$ and $d_1^2 > 3d_2$, or (ii) $d_2 < 0$ and $\Delta < 0$, then eqn. (A1) has positive simple roots.

where

$$\Delta = S(\varepsilon_1)S(\varepsilon_2) = \frac{4}{27}d_2^3 - \frac{1}{27}d_1^2d_2^2 - \frac{2}{3}d_1d_2d_3 + \frac{4}{27}d_1^3d_3 + d_3^2 \quad (A2)$$

with ε_1 and ε_2 being the two turning points of $S(\eta)$ given by

$$\varepsilon_1 = \frac{-d_1 - \sqrt{d_1^2 - 3d_2}}{3}, \varepsilon_2 = \frac{-d_1 + \sqrt{d_1^2 - 3d_2}}{3}. \quad (A3)$$

B. If $d_2 \geq 0$, the necessary condition for eqn. (A1) to have no positive

real roots are either

$$(i) \quad d_1^2 < 3d_2$$

$$(ii) \quad d_1^2 = 3d_2$$

$$(iii) \quad d_1^2 - 3d_2 > 0 \text{ and } \Delta > 0, \text{ or}$$

$$(iv) \quad d_1^2 - 3d_2 > 0 \text{ and } \Delta < 0, \quad d_1 > 0 \text{ and } d_2 > 0$$

Proof of this lemma is found in Khan and Greenhalgh [4].

Theorem 1. (Routh-Hurwitz Criteria). Let \mathbf{x}^* be an equilibrium point of eqn. (A4), and \mathbf{J} be the Jacobian evaluated at the equilibrium point. Suppose the diagonalization of \mathbf{J} yields the following characteristic equation

$$\lambda^3 + A\lambda^2 + B\lambda + C = 0. \quad (A6)$$

The equilibrium state \mathbf{x}^* will be local asymptotically stable if the coefficients A, B and C satisfy the following conditions:

$$A > 0,$$

$$C > 0$$

and

$$AB > C. \quad (A7)$$

Theorem II. (Hopf Bifurcation). Suppose the functions $F_i(\{\mathbf{x}\})$ depends on parameter $\tau \in \mathbb{R}$. The Jacobian will now depend on the parameter τ , i.e.,

$$J(\tau) = D_{\mathbf{x}} F(\mathbf{x}^*, \tau) = \frac{\partial F_i}{\partial \mathbf{x}_j}(\mathbf{x}^*, \tau) \quad i, j = 1, 2, \dots, n, \quad ,$$

If $J(\tau)$ has a pair of complex eigenvalues, $\lambda(\tau_0) = u(\tau_0) \pm iv(\tau_0)$ such that

$$i. \quad u(\tau_0) = 0,$$

$$ii. \quad v(\tau_0) = v^* > 0$$

and

$$iii. \quad \frac{du}{da}(\tau_0) \neq 0 \quad (A8)$$

where τ_0 is called a critical value of the bifurcation parameter ' τ ', and no other eigenvalues with zero real part exist, the system will undergo a transition to a limit cycle about the point (\mathbf{x}^*, τ_0) .

Proofs of this theorem can be found in various textbooks.²