Dynamical Analysis of a Discrete-time Plant-Larva-Adult (PLA) Model with Allee Effect on the Plant

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Abstract: In this paper, we formulate a discrete-time Plant-Larva-Adult (PLA) model with Allee effect on the plant population. We developed a model that captures the basic features of the interaction between a flowering plant and an insect with a larval stage that feeds on the plant's vegetative tissues (e.g. leaves) and an adult pollinator stage. The fixed points were computed and criteria for stability of the system were obtained. Time series plots were obtained for different sets of parameter values. The numerical simulations not only illustrate the validity of our results, but also exhibit more complex dynamical behaviours.

Keywords: Allee effect, PLA model, pollination, fixed points, stability analysis

1. Introduction

Mathematical modelling in population dynamics has gained a lot of attention and appreciation during the last few decades and among these models plant-herbivore system plays an important role. Mathematics is one way to explain many ideas and concepts in science. In the field of ecology, a lot of theoretical studies were carried out since the beginning of last century to explain the interaction between the ecological communities. The remarkable variety of dynamical behaviours exhibited by many species of plants, insects and animals has simulated great interest in the development of dynamical models of ecosystem. Ecosystem models are a development of theoretical ecology that aims to characterize the major dynamics of ecosystems, both to synthesise the understanding of such systems and to allow predictions of their behaviour. Research in theoretical ecology was initiated by Lotka and by Volterra [13, 20]. There are several theoretical outcomes for mutual dependence between plant and herbivore populations. Classical approaches for modelling plant-herbivore system have analogy with the prey-predator systems [15, 18].Plantherbivore interaction exhibit natural oscillations in the population of both plant and the herbivore. All the models for the coupled dynamics of consumer populations and limiting resources differ qualitatively according to their base-line assumptions about density-dependence in rates of birth and death of consumers and resources [6, 12, and 17]. For example, the persistence and stability of plant-herbivore population depend on how the consumption rate per herbivore changes with plant and herbivore density. In this paper, we aim to contribute a better understanding of the interplay between the plant-larva-adult models with Allee effect on the plant population.

The Allee effect is a phenomenon in biology named after Allee, who first wrote extensively on it [2]. It describes a positive relation between the population of a species density and its per capita growth rate at its low population densities, have great impacts in species establishment, persistence, invasion and evolutionary traits. Empirical evidence of Allee effect has been reported in many natural populations including plants, insects, marine invertebrates, birds and mammals. Various mechanisms at low population densities, such as the need of a minimal group size is necessary to successfully raise offspring, produce seeds, forage, and/or sustain herbivore attacks, or enhanced genetic inbreeding have been proposed as potential sources of the Allee effects [8-11]. Courchamp et al, described the Allee effect in a straight forward manner: "The more the merrier" [3]. This effect is simply a casual positive relationship between the number of individuals in a population and their overall individual fitness. Recently, many researchers have studied the impact of Allee effects on population interactions [22] as well as the interplay of Allee effects on species establishment and persistence [1, 14, 21]. One particular study describes the interaction between plant and herbivore population living in a closed environment with the two populations striving for survival.

Pollination is one of the most important mutualisms occurring between plants and insect herbivores. During the larval stage of many insect pollinators, such as Lepidopterans (butterflies and moths), the larvae feed on plant leaves to mature and become adult pollinators [19]. These ontogenetic diet shifts are very common and important in understanding the ecological and evolutionary dynamics of plant-animal mutualisms. Interestingly, in some cases larvae feed on the plant species, when they are adults they pollinate with the same plant species [5, 7]. This shows that in several cases mutualistic and antagonistic interactions are exerted by the same species, and a potential conflict arises within the plant, between the benefits of mutualism and the costs of herbivores. One of the best known examples is the interaction between tobacco plants (Nicotiana attenuata) and the hawk moth (Manduca sexta), whose larva is commonly called the tobacco hornworm [16]. There are other examples for this type of interaction, in the genus Manduca (Sphingidae), such as between the tomato plant (Lycopersicon esculentum) and the five spotted hawk moth (Manduca quinquemaculata). These larvae have received a lot of attention due to their negative effects on agricultural crops. In the pollination-herbivore cases, the role of an insect as a pollinator or herbivore depends on the stage in its life cycle. Thus, whether mutualism or herbivore dominates the interaction is dependent on insect abundance

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and its population structure. In other words the cost: benefit ratio must be positively related with the insect's larva: adult ratio.

This paper focuses the study of the relation between insect population structure, pollination and herbivore. Through this paper, we can understand the balance between costs (herbivory) and benefits (pollination) affects the interaction between plants and herbivore-pollinator insects and also what role does Allee effect play in balancing the resulting dynamics. We use a mathematical model which considers two different resources provided by the same plant species, nectar and vegetative tissues. Nectar consumption benefits the plant in the form of fertilized ovules, and consumption of vegetative tissues by larvae causes a cost. This model predicts that the balance between mutualism and antagonism, and the long term stability of the plant-insect association, can be greatly affected by changes in larval development rates, as well as by changes in the diet of adult pollinators.

2. Mathematical Model

This model concerns the dynamics of the interaction between a plant and an insect with Allee effect. The insect life cycle comprises an adult phase that pollinates the flowers and a larval phase that feed on non-reproductive tissues of the same plant. Flowers are ephemeral compared with plants and insects, so we consider that they attain a steady-state between production and disappearance. As a result, the dynamics is stated only in terms of plant, larva and adult populations, that is, the PLA model. The mechanism of interaction between plant, larva and adult is described by the following system of ordinary differential equations (ODE):

$$= rx\left(1 - \frac{x}{k}\right) - \beta xy + \sigma \left[\frac{\alpha z}{\omega + z}\right] x$$

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In order to study the stability of the fixed point model, we first give the following theorem.

Theorem:

dx dt

If $P(\lambda) = \lambda^2 + B\lambda^2 + C\lambda + D = 0$ is the characteristic equation of the matrix then the following statements is true:

- a) If every root of the equation has absolute value less than one, then the fixed point of the system is locally asymptotically stable and the fixed point is called a sink.
- b) If at least one of the roots of the equation has absolute value greater than one, then the fixed point of the system is unstable and the fixed point is called a saddle.
- c) If every root of the equation has absolute value greater than one, then the fixed point of the system is a source.
- d) The fixed point of the system is called hyperbolic if no root of the equation has absolute value equal to one. If there exists a root of equation with absolute value equal to one, then the fixed point is called Non-hyperbolic [4].

$$\frac{dy}{dt} = (1 - \gamma)y + \delta xy - \lambda yz \qquad (1)$$
$$\frac{dz}{dt} = (1 - \mu)z + \rho yz$$

The model parameters are described below:

- x, y and z: Plant, Larva and Adult biomass.
- *r* : Plant intrinsic growth rate.
- *k* : Carrying capacity.
- 3 : The herbivory rate.
- σ : Plant pollination efficiency ratio.
- *a* : Allee effect constant (i.e. pollination agent).
- ω : Half-saturation constant of pollination.
- γ : Larva mortality rate.
- δ : The rate of conversion of a consumed leaves to a larva.
- λ : Insect intrinsic reproduction rate.
- **p** : The herbivory rate.
- μ : Adult mortality rate.

2.1. Equilibrium Points

The system (1) has three equilibrium points which are i) $E_0 = (0,0,0)$

ii)
$$E_1 = \left(k\left[1-\frac{1}{r}\right], 0, 0\right)$$

iii) $E_2 = \left(\frac{\gamma}{\delta}, \frac{r}{\beta}\left[\frac{\delta k-\gamma}{\delta k}\right] - \frac{1}{\beta}, 0\right)$

3. The Dynamical behaviour of the model

In this section, we study the local behaviour of the system (1) about each equilibrium points. The stability of the system (1) is carried out by computing the Jacobian matrix point. The Jacobian

$$f(x, y, z) = \begin{bmatrix} r - \frac{2rx}{k} - \beta y + \sigma \left(\frac{az}{\omega + z}\right) & -\beta x & \frac{\sigma a \omega x}{(\omega + z)^2} \\ \delta y & 1 - \gamma + \delta x - \lambda z & -\lambda y \\ 0 & \rho z & 1 - \mu + \rho y \end{bmatrix}$$
 ------(2)

Proposition: 1

The equilibrium point E_0 is a

- (a) Sink if $r < 1, 0 < \gamma < 2$ and $0 < \mu < 2$;
- (b) Source if r > 1, $\gamma > 2$ and $\mu > 2$;
- (c) Saddle if r > 1, $0 < \gamma < 2$ and $0 < \mu < 2$;
- (d) Non-hyperbolic if r = 1 or $\gamma = 2$ or $\mu = 2$.

Proof:

In order to prove this result, we determine the eigenvalues of the Jacobian matrix J at E_0 . The Jacobian matrix evaluated at the equilibrium point E_0 has the form

$$J(E_0) = \begin{bmatrix} r & 0 & 0 \\ 0 & 1 - \gamma & 0 \\ 0 & 0 & 1 - \mu \end{bmatrix}$$

Hence the eigen values of the matrix $J(E_0)$ are $\lambda_1 = r$; λ_2 $= 1 - \gamma$; $\lambda_3 = 1 - \mu$. By using theorem, it is easy to see that, E_0 is a sink if r < 1, $0 < \gamma < 2$ and $0 < \mu < 2$; E_0 is a source if r > 1, $\gamma > 2$ and $\mu > 2$; E₀ is a saddle if r > 1, 0 < $\gamma < 2$ and $0 < \mu < 2$; and also E_0 is a non-hyperbolic if r = 1 or $\gamma = 2$ or $\mu = 2$.

Proposition: 2

The equilibrium point E_1 is a (a) Sink if 1 < r < 3; $r < \frac{\delta k}{\delta k - \gamma}$ and $0 < \mu < 2$; (b) Source if r > 3; $r > \frac{\delta k}{\delta k - \gamma}$ and $\mu > 2$; (c) Saddle if r > 3; $r < \frac{\delta k}{\delta k - \gamma}$ and $\mu < 2$;

Proof:

In order to prove this result, we determine the eigenvalues of the Jacobian matrix J at E_1 . The Jacobian matrix evaluated at the equilibrium point E_1 has the form

$$J(E_{1}) = \begin{bmatrix} 2 - r & \beta k \left(\frac{1}{r} - 1\right) & \frac{\sigma \alpha k (r-1)}{r \omega} \\ 0 & 1 - \gamma + \delta k \left(1 - \frac{1}{r}\right) & 0 \\ 0 & 0 & 1 - \mu \end{bmatrix}$$

Hence the eigen values of the matrix $J(E_1)$ are $\lambda_1 = 2 - r$; $\lambda_2 = 1 - \gamma + \delta k \left(1 - \frac{1}{r}\right)$; $\lambda_3 = 1 - \mu$. By using theorem, it is easy to see that, E_1 is a sink if 1 < r < 3; $r < \frac{\delta k}{\delta k - \gamma}$ and $0 < \mu < 2$; E_1 is a source if r > 3; $r > \frac{\delta k}{\delta k - \gamma}$ and $\mu > 2$; and finally E_1 is a saddle if r > 3; $r < \frac{\delta k}{\delta k - \gamma}$ and $\mu < 2$.

Proposition: 3

The equilibrium point E_2 is a (a) Sink if $\frac{\delta k}{\delta k-\gamma} < r < \frac{\delta k (\beta \mu + \rho)}{\rho (\delta k-\gamma)}$ (b) Source if $\frac{\delta k (\beta \mu + \rho)}{\rho (\delta k-\gamma)} < r < \frac{\delta k}{\delta k-\gamma}$; (c) Saddle if $r > \frac{\delta k (\beta \mu + \rho)}{\rho (\delta k-\gamma)}$ and $r > \frac{\delta k}{\delta k-\gamma}$.

Proof:

In order to prove this result, we determine the eigenvalues of the Jacobian matrix J at E_2 . The Jacobian matrix evaluated at the equilibrium point E_2 has the form

$$J(E_2) = \begin{bmatrix} 1 - \frac{\gamma \gamma}{k\delta} & \frac{-\rho \gamma}{\delta} & \frac{\delta u \gamma}{\omega \delta} \\ \frac{r(\delta k - \gamma) - \delta k}{\beta k} & 1 & \frac{\lambda}{\beta} - \frac{\lambda r(\delta k - \gamma)}{\beta \delta k} \\ 0 & 0 & 1 - \mu + \frac{\rho r(\delta k - \gamma)}{\beta \delta k} - \frac{\rho}{\beta} \end{bmatrix}$$

Hence the eigen values of the Jacobian matrix $J(E_2)$ are $\lambda_1 = \left[1 - \mu + \frac{\rho r(\delta k - \gamma)}{\beta \delta k} - \frac{\rho}{\beta}\right];$

$$\begin{split} \lambda_{2,3} &= \left(1 - \frac{r\gamma}{2\delta k}\right) \pm \frac{1}{2} \sqrt{\frac{r^2 \gamma^2}{\delta^2 k^2} - \frac{4\gamma \delta^2 r}{\beta \lambda} + \frac{4\gamma^2 \delta}{\beta \lambda k} + \frac{4\gamma \delta^2 k}{\beta \lambda}} \text{ . By using} \\ \text{theorem, it is easy to see that, } E_2 \text{ is a sink if} \\ \frac{\delta k}{\delta k - \gamma} &< r < \frac{\delta k \left(\beta \mu + \rho\right)}{\rho \left(\delta k - \gamma\right)} \text{ ; } E_1 \text{ is a source if} \\ \frac{\delta k \left(\beta \mu + \rho\right)}{\rho \left(\delta k - \gamma\right)} < r < \frac{\delta k}{\delta k - \gamma} \text{ ; and finally } E_1 \text{ is a saddle if} \\ r > \frac{\delta k \left(\beta \mu + \rho\right)}{\rho \left(\delta k - \gamma\right)} \text{ and } r > \frac{\delta k}{\delta k - \gamma} \text{ .} \end{split}$$

4. Numerical Analysis

In this section, we illustrate the analytical findings with the help of numerical simulations performed with MATLAB programming. We present time series plots for system (1) to confirm the theoretical results with hypothetical set of data. They show interesting complex dynamical behaviours.

Case: 1

We shall consider r = 0.15, k = 1, $\beta = 0.15$, $\sigma = 0.5$, $\alpha = 0.5$, $\omega = 0.1$, $\gamma = 0.1$, $\delta = 0.15$, $\lambda = 0.04$,

 $\mu = 0.95$ and $\rho = 0.94$. At equilibrium point $E_0 = (0, 0, 0)$, the eigenvalues are $\lambda_1 = 0.15$, $\lambda_2 = 0.9$, $\lambda_3 = 0.05$ so that $|\lambda_{1,2,3}| < 1$. Hence the trivial equilibrium point is stable (see Figure: 1).

Case: 2

We shall consider r = 1.1, k = 1, $\beta = 0.65$, $\sigma = 0.5$, $\alpha = 0.5$, $\omega = 0.1$, $\gamma = 0.1$, $\delta = 0.5$, $\lambda = 1.14$, $\mu = 0.5$ and $\rho = 0.4$. The equilibrium point E₁ = (0.0909, 0, 0) and the eigenvalues are $\lambda_1 = 0.9$, $\lambda_2 = 0.945$, $\lambda_3 = 0.5$ so that $|\lambda_{1,2,3}| < 1$. Hence system (1) is stable (see Figure: 2).

Case: 3

We shall consider r = 1.5, k = 1, $\beta = 0.65$, $\sigma = 0.5$, $\alpha = 0.5$, $\omega = 0.1$, $\gamma = 0.1$, $\delta = 0.5$, $\lambda = 1.14$, $\mu = 0.5$ and $\rho = 0.4$. The equilibrium point E₂ = (0.2, 0.3076, 0) and the eigenvalues are $\lambda_1 = 0.62$, $\lambda_2 = 0.95$, $\lambda_3 = 0.74$ so that $|\lambda_{1,2,3}| < 1$. Thus system (1) is stable (see Figure: 3).

5. Discussion

We developed a plant-larva-insect model with Allee effect on the plant that considers two interaction types, pollination and herbivory. In particular case, interaction types depend on the stage of the insect's life cycle as inspired by the interaction between Manduca sexta and Datura wrightii or the interaction between Manduca sexta and Nicotiana attenuata. The parameters in this analysis can change due to external factors. One of the most important is temperature. Flowering, pollination, herbivory, growth and mortality rates are temperature-dependent and they can increase with warming depending on the thermal impacts on insect and plant metabolisms. However, we get the general picture that warming or cooling can change the balance between costs and benefits impacting the stability of the plant-insect association.

Some pesticides are hormone retarding agents. This means that their release can reduce maturation rates, altering the balance of the interaction towards more herbivory and less pollination and finally endangering pollination service. Another factor that can increase or decrease larvae maturation rates, is the level of nutrients present in the plant's vegetative tissue. An important factor that can affect the balance between mutualism and herbivory is the diet breadth of pollinators. From the lack of alternative pollinators could also lead to increase herbivory and loss of stability.

6. Conclusion

Many insect pollinators are herbivores during their larval phases. If pollination and herbivory targets the same plant (e.g. as between tobacco plants and hawk moths), the overall outcome of the association depends on the balance between costs and benefits for the plant. We proved that system (1) has a unique positive equilibrium point, which is locally asymptotically stable. The main objective of dynamical system is to predict the global behaviour of a system based on the knowledge of its present state. An approach to this problem consists of determining the possible global behaviours of the system and determining which initial conditions lead to these long-term behaviours.

Due to the simplicity of our PLA model with Allee effect, we have carried out a systematic, local and global stability analysis of it. Particularly, the condition for local asymptotic stability in population biology is a very interesting mathematical problem. Usually the biologists believe that a unique, positive, locally asymptotically stable equilibrium point in an ecological system is very important in biological point of view. Therefore, it is very important to find conditions which may guarantee the local asymptotic stability of the unique positive equilibrium point of the given system. In this paper, we proved the necessary and sufficient condition for the local asymptotic stability of the unique positive equilibrium point of system (1). Some numerical examples were provided to support theoretical results.

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Author Profile



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years of teaching experience and now he is working in Sri Subramaniya Swami Government Arts College, Tiruttani. His areas of research are Drug designing, Mathematical models in Prey-Predator system, Plant-Herbivore system and Queuing system. He has published 16 international journals, presented 7 research papers in various National and International Conferences. He has supervised 15 M.Phil, scholars in the area of various Queuing models. He has also given invited talks in National and International conferences in his specialized areas.

PLANT – LARVA - ADULT 8 P 5 ADULT ADULT PLANT – LARVA ADULT LARVA ARVA * PLANT * * * * * * * ↓ PLANT 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0 TIME TIME Figure: 1 Figure: 2 Time series graph for PLA model with Allee effect Time series graph for PLA model with Allee effect $(r = 0.15, k = 1, \beta = 0.15, \sigma = 0.5, \alpha = 0.5, \omega = 0.1, \gamma = 0.1,$ $(r = 1.1, k = 1, \beta = 0.65, \sigma = 0.5, \alpha = 0.5, \omega = 0.1,$ $\delta = 0.15, \lambda = 0.04, \mu = 0.95 \text{ and } \rho = 0.94.)$ $\gamma = 0.1$, $\delta = 0.5$, $\lambda = 1.14$, $\mu = 0.5$ and $\rho = 0.4$.) - ADULT ADULT PLANT - LARVA LARVA * PLANT



Appendix: