A delayed plant-herbivore model with a strong Allee effect in plant population

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Abstract. The article accommodates a delayed plant-herbivore model consolidating the strong Allee effect with intraspecific competition among herbivores. The Holling type-*II* functional response is utilized which describes that an individual predator consumes food till it feels famished. The time delay (τ) is also considered in the model due to which the equilibrium losses stability. The associated state variables are: plant population and herbivore population. The non-trivial equilibrium point is calculated for the strong Allee effect. It is observed that the system is stable about the non-trivial equilibrium. The observation of Hopf- bifurcation is shown at the crucial value of the time delay. Moreover, it is found that the entire system becomes more and more stable while the intraspecific competition rate of herbivores (δ) keeps on increasing as represented in time series graphs. The analytical results are shown graphically with the help of MATLAB software to illustrate the proposed mathematical model.

Keywords: *Plants; Herbivores; Strong Allee effect; Functional response; Hopf- bifurcation.*

1   Introduction

The field of applied mathematics considers mathematical modelling for a variety of biological issues to be an interesting research area. In the biological field, predator-prey systems that can exhibit interactions between prey-predator species play a vital role. In 1920, the theory of predator-prey mathematical modelling was first developed. Lotka [1], from the United States, and Volterra [2], were the first to develop the predator-prey model. Plant-herbivore dynamics are frequently depicted by modified versions of the Lotka-Volterra predator-prey model [3]–[5]. Warder Allee invented the Allee effect in the 1930s [6]. If the growth rate at low density is positive in the first instance, then the population has an impact on the Allee effect [7], [8]. The Allee effect usually occurred due to the challenges in searching for mates, feeding habits, interaction with society, predator satiation, and cooperative defense, among other factors [9], [10]. The categories of the Allee effect are the Strong and Weak Allee effects. A strong Allee effect introduces a threshold value of the population size and the population's per capita growth rate is negative below the threshold value. However, if the population's growth rate remains positive but decreases when the population densities are low, then it is categorized as the weak Allee effect [11]–[13]. The dynamics of the plant-herbivore population under both the Allee effects with Holling-type I functional response is proposed. Under the strong Allee effect, the plants and herbivores population vanishes. Under the weak Allee effect, Hopf-bifurcation is seen [14]. In 1959,

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Holling introduced the theory of functional response. A functional response is an immediate change in the rate at which it consumes prey in response to prey abundance [15]–[17]. $P(x) = kx$ gives the Holling type-I functional response, where $x(t)$ is the prey biomass and k is constant and always positive. A saturation function is applicable to explain the consumption of food because the Holling type-II response incorporates that an individual predator consumes food till it feels famished. Therefore, the functional response is: $P(x) = kx/(1 + T_h kx)$; here $x(t)$ is the prey biomass and k is searching efficiency which is always positive and T_h is average time for each prey [10]. The occurrence of delay differential equations in the plant–herbivore dynamics is a result of herbivore damage [18]–[20]. Using a system of non-linear delay differential equations, the impact of time lag on the extinction of toxicant-affected plant population has been investigated [21]–[23]. Under the inhibitory and stimulatory allelopathic effects, the aspect of delay parameter in the plant population has been examined [24], [25].

Many researchers have studied the plant-herbivore dynamics with or without Allee effect. However, the utilization of delay differential equations imposed by the Allee effect has been studied rarely. Therefore, in this article, Plant herbivore dynamics with Holling type-II functional response imposed by strong Allee effect is considered.

2   Mathematical Model

In this paper, the associate variables $P(t)$ and $H(t)$ stands for Plant population and Herbivore population respectively. The variables used in the model are positive i.e., $P(t) > 0$ and $H(t) > 0$ and $0 < b < C$ for strong Allee effect. The reproduction of herbivores is not immediate to the intake of plants. There is an essential delay in gestation. Therefore, time delay (τ) has been introduced in the proposed model.

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{C}\right)(P - b) - \frac{a_1 PH}{P + m} \tag{1}$$

$$\frac{dH}{dt} = \frac{a_2 P(t-\tau)H}{P(t-\tau)+m} - dH - lH^2 \tag{2}$$

Variables/Parameters	Description
r	The internal growth rate of plants
C	Carrying capacity
b	Survival threshold of the plants
a_1	Capturing rate
$a_2 = (ea_1)$	Conversion rate
m	Half-capturing saturation constant
d	The death rate of herbivores
l	Intraspecific competition rate of herbivores
τ	Time delay

Table 1. Details of the system parameters (1)-(2).

3   Non- dimensionalization

To curtail the number of parameters, let

$$\frac{rt'}{b} = t \, , \frac{P}{C} = x' \, , \frac{a_1 H}{a_2 C} = y'$$

and then dropping the dashes for simplicity, the model becomes:

$$\frac{dx}{dt} = x(1-x)\left(1-\frac{x}{M}\right) - \frac{\alpha xy}{x+\gamma} \tag{3}$$

$$\frac{dy}{dt} = \frac{\alpha x(t-\tau)y}{x(t-\tau)+\gamma} - \beta y - \delta y^2 \tag{4}$$

where the dimensionless parameters are

$$M = \frac{b}{c} \, , = \frac{m}{c} \, , \alpha = \frac{a_2 b}{r} \, , \beta = \frac{db}{r} \text{ and } \delta = \frac{la_2}{rba_1}.$$

4   Non-trivial Equilibrium of the model $E^*(P^* \neq 0, H^* \neq 0)$

This section accommodates the non-trivial equilibrium which depicts the co-existence of the state variables (P^*, H^*), where these state variables are not equal to zero. The stability of the system represents no impact of time delay on any of the other equilibrium points, therefore only non-trivial equilibrium is calculated. To calculate the feasible non-trivial equilibrium, equate the system of equations (1) and (2) to zero at $E^*(x^* \neq 0, y^* \neq 0)$, $x^*(t-\tau) \approx x^*(t)$:

$$\frac{dx^*}{dt} = 0 \Rightarrow y^* = \frac{(1-x^*)(M-x^*)(x^*+\gamma)}{\alpha M}, \text{ provided } 1, M > x^*$$

Here, the quartic equation has a positive root x^*.

And

$$\frac{dy^*}{dt} = 0$$

$$\Rightarrow x^{*4} + k_1 x^{*3} + k_2 x^{*2} + k_3 x^* + k_4 = 0$$

where

$$k_1 = 2\alpha + L - 1, \text{ provided } 2\alpha + L > 1;$$

$$k_2 = \alpha^2 - 2\alpha - 2\alpha L + L, \text{ provided } L > \alpha^2 - 2\alpha - 2\alpha L;$$

$$k_3 = \frac{L[\beta(\beta-\gamma)+\alpha\delta(2-\alpha)]-\delta\alpha^2}{\delta},$$

$$\text{provided } \beta > \gamma, 2 > \alpha \text{ and } L[\beta(\beta-\gamma)+\alpha\delta(2-\alpha)] > \delta\alpha^2;$$

And $k_4 = \frac{\alpha L(\delta\alpha-\gamma\beta)}{\delta}$, provided $\alpha > \frac{\gamma}{\delta}\beta$

5   Stability Analysis and Hopf- Bifurcation

The set of Eqs. (3)-(4) of a delayed plant-herbivore model under the strong Allee effect about $E^*(x^*, y^*)$ are equivalent to:

$$\frac{dx^*}{dt} = x^*(1 - x^*)\left(1 - \frac{x^*}{M}\right) - \frac{\alpha x^* y^*}{x^* + \gamma} \tag{5}$$

$$\frac{dy^*}{dt} = \frac{\alpha x^*(t-\tau) y^*}{x^*(t-\tau) + \gamma} - \beta y^* - \delta y^{*2} \tag{6}$$

The exponential equation of the above system is

$$(\lambda^2 + l\lambda + m) + e^{-\lambda\tau} n = 0 \tag{7}$$

Where $l = \left[\frac{\alpha\gamma y^*}{(x^*+\gamma)^2} - \frac{x^*(3x^*-2M-2)}{M} + 2\delta y^* + \beta - 1\right]$;

$$m = (\beta + 2\delta y^*)\left[\frac{\alpha\gamma y^*}{(x^*+\gamma)^2} - \frac{x^*(3x^*-2M-2)}{M} - 1\right];$$

And $n = \frac{-\alpha^2 \gamma x^* y^*}{(x^*+\gamma)[x^*(t-\tau)+\gamma]^2}$

If $\tau = 0$, then the Eq. (7) becomes:

$$\lambda^2 + l\lambda + (m + n) = 0 \tag{8}$$

By the criteria [26], the system is stable, i.e., roots of the Eq. (8) will have its real part as negative when:

$(\boldsymbol{h_1})$: $l > 0$;

$(\boldsymbol{h_2})$: $(m + n) > 0$

which clearly holds.

Further, we investigate the transference of the real part of the roots which is negative to the real part which is positive with alteration in the values of time delay (τ).

Consider, Eq. (7) has a root $\lambda = i\omega$:

$$(i\omega)^2 + l(i\omega) + m + ne^{-(i\omega)\tau} = 0$$

$$\Rightarrow -\omega^2 + l(i\omega) + m + n(\cos\omega\tau - i\sin\omega\tau) = 0$$

Segregating real and imaginary parts:

$$\omega^2 - m = n\cos\omega\tau \tag{9}$$

$$l\omega = n\sin\omega\tau \tag{10}$$

Squaring and adding:

$$\omega^4 + (l^2 - 2m)\omega^2 + (l^2 - n^2) = 0 \tag{11}$$

The two roots of Eq. (11) are:

$$\omega_{1,2}^2 = \frac{(2m-l^2)\pm[(l^2-2m)^2 - 4(l^2-n^2)]^{1/2}}{2} \tag{12}$$

The two roots $\omega_{1,2}^2$ are not positive if:

$(\boldsymbol{h_3})$: $(2m - l^2) < 0$ *and* $(l^2 - n) > 0$ *or* $(l^2 - 2m) < 4(l^2 - n^2)$

Therefore, if the condition (h_3) holds, then the Eq. (12) does not have positive roots.

There are the following two Conjectures [26].

Conjecture A. If $(h_1) - (h_2)$ is true, then each root of the Eq. (7) have real parts which are negative for all $\tau \geq 0$.

On the contrary, when:

$$(h_4): (l^2 - n^2) < 0 \; or \; (2m - l^2) > 0 \; and \; (l^2 - 2m)^2 = 4(l^2 - n^2)$$

Then, the positive root of Eq. (9) is ω_1^2.

$$(h_5): (l^2 - n^2) > 0 \; or \; (2m - l^2) > 0 \; and \; (l^2 - 2m)^2 > 4(l^2 - n^2)$$

Then, two positive roots of Eq. (9) are $\omega_{1,2}^2$.

For some specific values of τ, roots of Eq. (7) are purely imaginary in both- (h_4) and (h_5). The crucial values $\tau_j^{\pm}$ of τ can be enumerated from the set of Eqs. (9)-(10):

$$\tau_j^{\pm} = \frac{1}{\omega_{1,2}} \cos^{-1}\left(\frac{\omega_{1,2}^2 - m}{n}\right) + \frac{2j\pi}{\omega_{1,2}}, j = 0,1,2,3,4, \dots \tag{13}$$

The above preceding can be summarised in the following Conjecture B [26].

Conjecture B. (1) The roots of Eq. (7) are purely imaginary $\pm i\omega_1$, when $(h_1) - (h_2) \; and \; (h_4)$ is true and $\tau = \tau_j^{+}$.

(2) The roots of Eq. (7) are purely imaginary $\pm i\omega_1 (\pm i\omega_2 \; respectively)$, when $(h_1) - (h_2) \; and \; (h_5)$ is true and $\tau = \tau_j^{+}(\tau = \tau_j^{-} \; respectively)$.

The expectancy is that the displacement of the real part of some roots of Eq. (7) which are negative to the real part which is positive when $\tau > \tau_j^{+}$ and $\tau < \tau_j^{-}$. Consider the following to investigate the option:

$$\tau_j^{\pm} = \mu_j^{\pm}(\tau) + i\omega_j^{\pm}(\tau); j = 0,1,2,3,4, \dots$$

$$\mu_j^{\pm}\left(\tau_j^{\pm}\right) = 0, \omega_j^{\pm}\left(\tau_j^{\pm}\right) = \omega_{1,2}$$

is satisfied by the roots of Eq. (7).

The following transversality conditions can be verified:

$$\frac{d}{d\tau}\left(Re \; \lambda_j^{+}\left(\tau_j^{+}\right)\right) > 0 \; and \; \frac{d}{d\tau}\left(Re \; \lambda_j^{-}\left(\tau_j^{-}\right)\right) < 0$$

Hence, the nature of the bifurcating values $\tau_j^{\pm}$ given by the above expression is discussed in the detail by [26].

6   Graphical Simulation

To consolidate the analytical results, the following parametric values are taken into consideration to depict the dynamics graphically by the set of Eqs. (1)- (2).

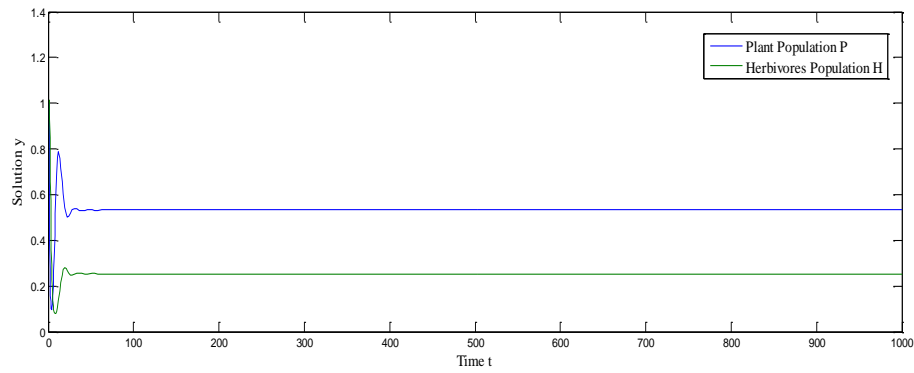$$\alpha = 1.65, \gamma = 0.5, \beta = 0.8, \delta = 0.2, M = 4.$$

Figure 1. When the system is without time delay (*i. e.*, $\tau = 0$), then E* (0.5322, 0.2537) is absolutely stable.
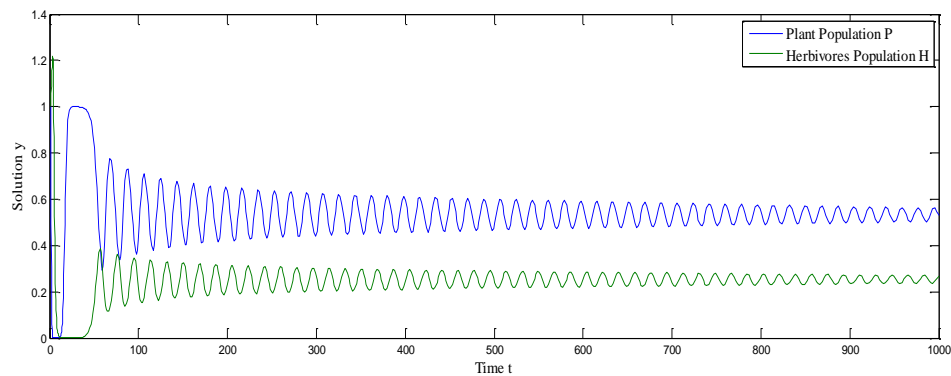

Figure 2. When the time delay is below the crucial value which is 2.7 (*i. e.*, $\tau < 2.7$), then E*(0.5520, 0.2553) is asymptotically stable.
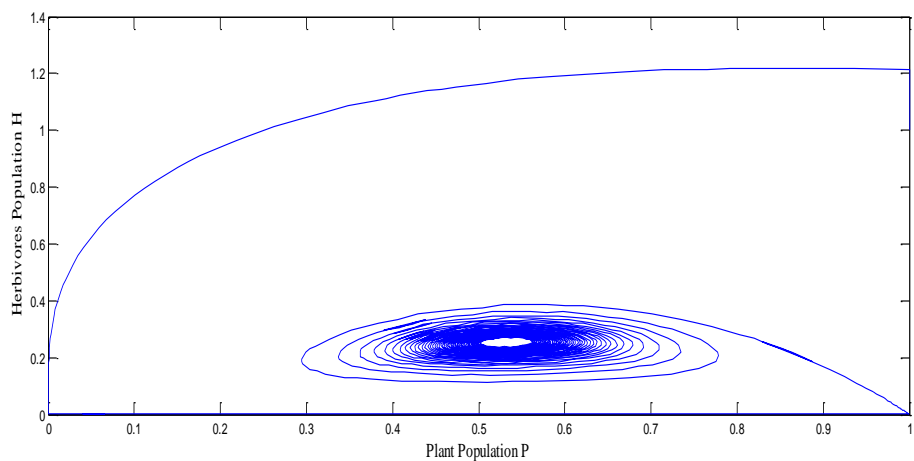

Figure 3. Phase space diagram showing the asymptotic stability of equilibrium E* (0.5520,0.2553), when the time delay is below the crucial value which is 2.7 (*i. e.*, $\tau < 2.7$.
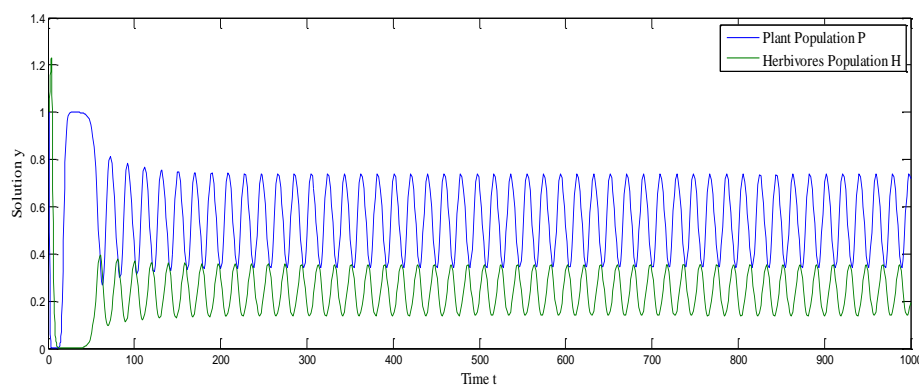
Figure 4. When the time delay surpasses the crucial value which is 2.7 (*i.e.*, $\tau \geq 2.7$), then E* (0.7276,0.1444) surrenders its stability, and limit cycles are seen, and hence Hopf- bifurcation.
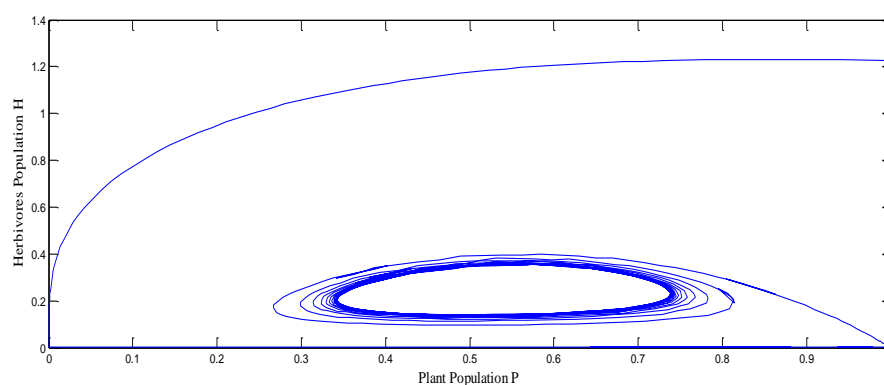

Figure 5. Phase space diagram showing the Hopf- bifurcation of equilibrium E* (0.7276, 0.1444) when the time delay surpasses the crucial value which is 2.7 (*i.e.*, $\tau \geq 2.7$).

7   Sensitivity Analysis

The research that represents the stability behaviour of the system while triggering the model parameters other than the time delay (τ) is known as Sensitivity analysis. The Direct method is used for this purpose. For an illustration, the sensitivity equations of the partial derivatives of the solution (P, H) with respect to the intraspecific competition rate of herbivores (δ) are given below:

$$\frac{dS_1}{dt} = \left[1 - 2\left(1 + \frac{1}{M}\right)x - \frac{3}{M}x^2 - \frac{\alpha xy}{(x+\gamma)^2}\right]S_1 - \frac{\alpha x}{x+\gamma}S_2 \tag{14}$$

$$\frac{dS_2}{dt} = \left[\frac{\alpha x(t-\tau)}{[x(t-\tau)+\gamma]} - \beta - 2\delta y\right]S_2 + \frac{\alpha xy}{[x(t-\tau)+\gamma]^2}S_1(t-\tau) \tag{15}$$

Where $S_1 = \frac{\partial x}{\partial \delta}$ and $S_2 = \frac{\partial y}{\partial \delta}$

7.1   Sensitivity of Variables to Parameter δ

When we increase the value of the intraspecific competition rate of herbivores (δ) from $\delta = 0.2$ to $\delta = 0.23$, then the state variables (P, H) shift its behaviour from Hopf-bifurcation to asymptotic stability. Again, when we increase $\delta = 0.23$ to $\delta = 0.25$, eventually, as

depicted in figs 6 and 7, the entire system shifts its dynamics from asymptotic stability to absolute stability.
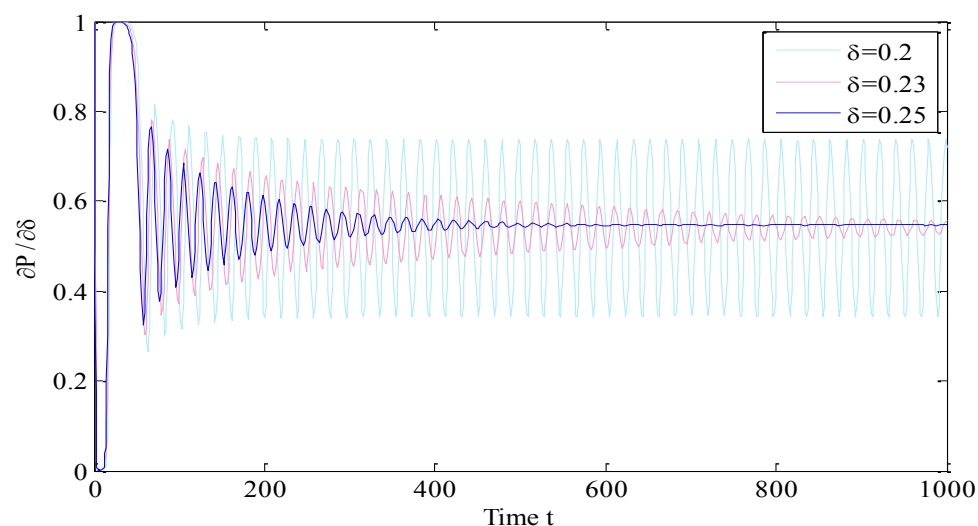

Figure 6. Time series graph of change in the size of plant population P with respect to changes in the intraspecific competition rate of herbivores (δ).
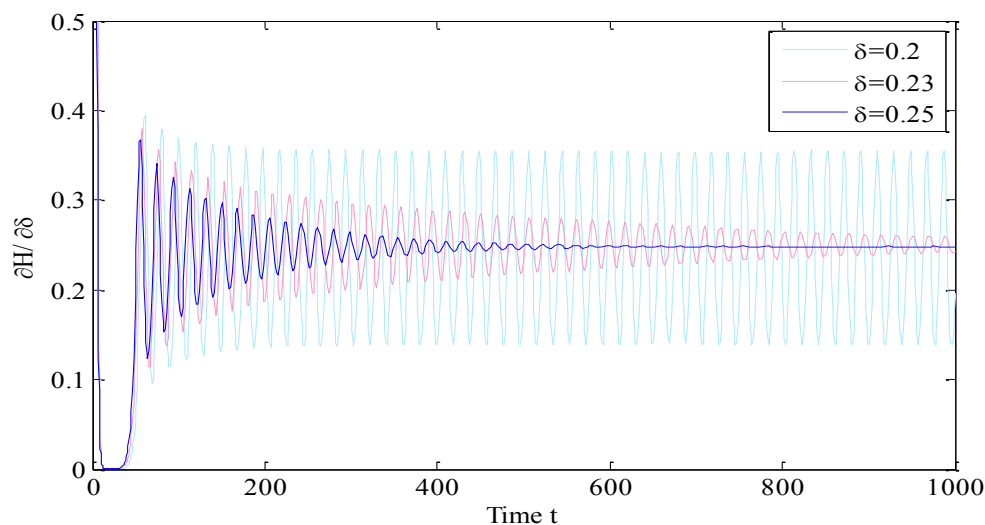

Figure 7. Time series graph of change in the size of herbivore population H with respect to changes in the intraspecific competition rate of herbivores (δ).

8   Conclusion

The proposed mathematical model represented the plant-herbivore dynamics using Holling Type-II functional response with intraspecific competition among herbivores. The strong Allee effect and time delay (τ) are incorporated in the model. The non-trivial equilibrium points E^* and stability of the system about E^* under strong Allee effect are examined. Fig 1 indicates that $E^*(0.5322, 0.2537)$ is absolutely stable, without time delay ($\tau = 0$). When the time delay is below 2.7 ($\tau < 2.7$), where 2.7 is a crucial value and keeping all the other parameters same, then $E^*(0.5520, 0.2553)$ is asymptotically stable which is shown by fig 2 and fig 3. When the time delay passes through the crucial value ($\tau \geq 2.7$), then

$E^*(0.7276, 0.1444)$ surrenders its stability and Hopf- bifurcation occurred as shown in fig 4 and fig 5.

Additionally, fig 6 and fig 7 indicate the change in the model parameters with respect to changes in the intraspecific competition rate of herbivores (δ) using time series graphs. It is found that when there is an increment in the value of the intraspecific competition rate of herbivores (δ) from $\delta = 0.2$ to $\delta = 0.23$, then the state variables which include the size of plant population and size of herbivore population (P, H) changes its behaviour from Hopf-bifurcation to asymptotic stability. Similarly, when there is an increment in the value of $\delta = 0.23$ to $\delta = 0.25$, the entire system again shifts its dynamics from asymptotic stability to absolute stability. Hence, when we keep on increasing the value of the intraspecific competition rate of herbivores, it is favourable for both the populations and the entire system tends to become more and more stable.

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