A model of plant-herbivore interaction with size structure in plants using toxin-determined functional response

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July 25, 2013

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Abstract

One of the possible consequences of global warming in the northern hemisphere is the invasion of Arctic Tundra by woody plants, which is influenced by the chemical defense of plants against mammal browsing. In this paper, we explore the toxin-mediated plant-herbivore interaction with size structure in plants using a simplified mathematical model. The size structure of plants is important as it seems to play a significant role on the woody plant invading. We formulate a three dimensional ordinary differential equations model of the simplified dynamics of adult-trees, seedlings and herbivores in the presence of chemical defense of plants, building on a general two dimensional toxin-determined functional response model of plants and herbivores. Then we investigate the mathematical features of the model, analyze the stability of equilbiria. When choosing plant toxin measurement G and herbivore health measurement μ as bifurcation parameters, we analytically show the existence of different bifurcations, including a saddle-node bifurcation and a Hopf bifurcation. A Bogdanov-Takens cusp with codimension 2 is also identified. A Bogdanov-Takens bifurcation occurs when bifurcation parameters are perturbed at the cusp.

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1 Introduction

One possible consequence of global warming is that the invasion of Arctic tundra area by the woody plants. But this woody plants invasion does not preceed uniformly along the timberline of tundra and woody plants in Arctic area, which might be explained by the chemical defense of invading woody plants against herbivory [3]. The selective mammal browsing on the less toxic woody plants retards the progression of invading while more toxic plants invade fast due to less damage of browsing in the case study [3] on different types of birch, genus *Betula*, with different intense of toxin defense. The purpose of this paper is to formulate a mathematical model to study the process of the invasion problem quantitatively. The plant toxin defense has been studied both in biologically orientated paper [5, 4, 7, 1, 22, 2, 23, 25, 21, 8, 24] and quantitatively in [16, 17, 10, 11, 15, 14, 12, 18, 9, 19]. The general model of one plant species and one herbivore population with toxin-determined functional response (referred to TDFRM) has been studied in [10, 17, 6], in which the negative effect of plant toxin was incorporated into Holling Type II functional response. The study of the frame work of the two dimensional system of ordinary differential equations presented rich dynamics [17], including saddle-node bifurcation, Hopf bifurcation and codimension 2 Bogdanov-Takens bifurcation, more complicated than the model with traditional Holling type II model. The regeneration of boreal woody plants is characterized by the size structure from young seedlings to adult trees after the seed production, dispersal and germination [13]. The size structure of plants might be an important factor in the woody plants invasion of tundra. However, to our best knowledge, the size structure of plants has not been explicitly modeled jointly with the effect of plant toxicity in previous studies.

In this paper, we shall build up a plant size-structured model of one plant species and one herbivore population. To setup the model, we have a few assumptions based on biological facts. We assume that mammal browsers do not feed on the adult trees. First, herbivores are not able reach the adult trees. As the adult trees grow larger, they have less leaves or twigs available to herbivores. Second, the concentration of toxin chemicals of adult plants is higher than that of seedlings. Liu et al.[18, 19] introduced a model with age structure of twigs, twigs at different ages have different toxin levels. So adult trees are also less preferred by herbivores.

The growth of adult trees consists of two parts. One part is self-growth, which means after seedlings become the adult trees, continue to grow larger and saturate at a certain level due to crowding effect. The other part of growth is new recruitment from the seedlings compartment. For seedlings, the new recruitment is assumed to be proportional to the adult trees, but we emphasize that the process of the reproduction is that the adult trees produce seeds proportional to their density and then seeds can germinate and grow into seedlings with a small probability. The seedlings grow up to adult trees at a constant rate per capita. Therefore, the model we study here is listed below:

$$\begin{aligned} \frac{dA(t)}{dt} &= rA - \gamma A^2 + bS, \\ \frac{dS(t)}{dt} &= pA - bS - C(S)H, \\ \frac{dH(t)}{dt} &= \beta C(S)H - \mu H. \end{aligned} \tag{1}$$

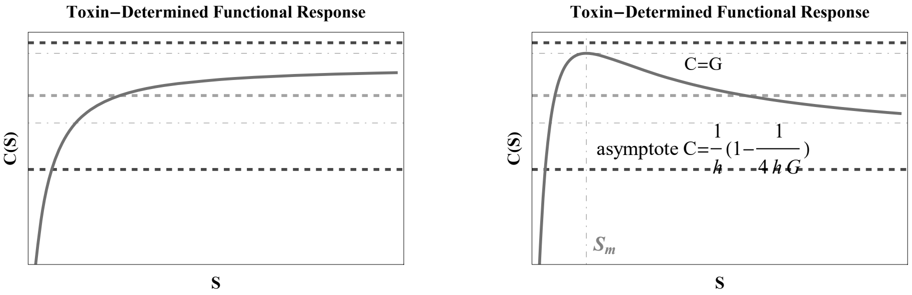
where

$$C(S) = f(S)\left(1 - \frac{f(S)}{4G}\right), \tag{2}$$

and

$$f(S) = \frac{e\sigma S}{1 + he\sigma S} \tag{3}$$

is the Holling Type 2 functional response for foraging on the plant species. The parameter e in equation (3) is the encounter rate of the plant resource, which depends on the movement velocity of the consumer and its radius of detection of food items, and also depends on the abundance of food resources. The parameter σ ($0 < \sigma \leq 1$) is the fraction of food biomass encountered that the herbivore ingests. The parameter h is the handling time per unit plant biomass, which incorporates the time required for the digestive tract to handle the item. The second part of the toxin-determined functional response $C(S)$ in (2), that is, $1 - f(S)/4G$, accounts for the negative effect of toxin, where $G = M/T$. The parameter M is a measure of the maximum amount of the plant toxicant per unit time that the herbivore can tolerate, and T is the amount of toxin per unit plant biomass. G decreases when the concentration of toxin tolerated by the herbivore decreases (high toxicity) or the concentration of toxin in the plant biomass increases. Therefore, the smaller the value of G, the larger the effect the toxin has on intake. The factor 4 is for mathematical purpose, which is a multiplier which guarantees that C as a function of S is nonnegative and does not exceed G. The parameters d denote the death rate of herbivore, including



(a) Monotone, $\frac{1}{2h} < G < \frac{1}{h}$ (b) Unimodal, $\frac{1}{4h} < G < \frac{1}{2h}$

Figure 1: Toxin-Determined Functional Response, (a) $C(S)$ is monotonically increasing in S if $\frac{1}{2h} < G < \frac{1}{h}$, (b) $C(S)$ is unimodal and reaches its maximum at $S_m = \frac{2G}{e\sigma(1-2Gh)}$ if $\frac{1}{4h} < G < \frac{1}{2h}$.

the natural death, predation and human hunting induced death and its value can vary representing management policies. The $C(S)$ could be monotone as shown in Figure 1(a), or could be unimodal as in Figure 1(b). In this paper we study the nonmonotone case of $C(S)$.

This paper is organized as follows. In section 2, we study the properties of the model (1). Section 3 presents the stability analysis of both boundary and interior equilibria, and investigates saddle-node bifurcation and Hopf bifurcation and shows the degenerated case at the intersection of two bifurcation curves, which is a codimension 2 Bogodanov-Takens cusp. In section 4, we summarize the results and the future works.

2 Analysis of the model

2.1 Properties of the Adult Trees-Seedlings system

Without the herbivores, the 2D system of adult trees-seedlings becomes as follows

$$\begin{aligned} \frac{dA(t)}{dt} &= rA - \gamma A^2 + bS, \\ \frac{dS(t)}{dt} &= pA - bS, \end{aligned} \tag{4}$$

Proposition 2.1. *The set* $\{(A,S)\,|\,0 \le A \le A_M,\ 0 \le S \le S_M\}$ *is positively invariant under 2D system (4). The system has two equilibrium points,* $E_0 = (0,0)$ *and* $E_M = (A_M, S_M)$*. Moreover,* E_0 *is always a saddle, unstable, and*

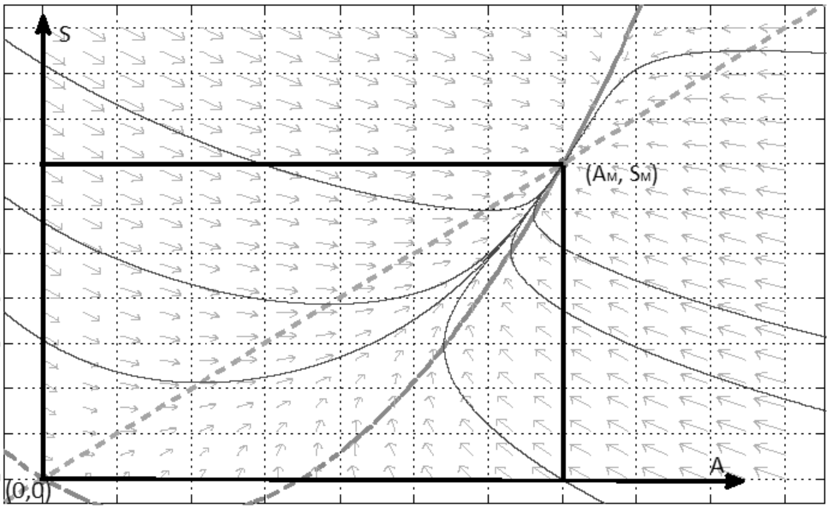


Figure 2: Phase portrait of the 2D system of adult trees and seedlings. The dashed curve are nullclines. $(0, 0)$ and (A_M, S_M) are the equilbiria of the 2D system (4). From the phase portrait, the equilibrium $(0, 0)$ is unstable, and the equilibrium (A_M, S_M) is stable and global attractive in the first quadrant. The rectangular region $[0, A_M] \times [0, S_M]$ is a globally attractor.

E_M is always stable nodes.

It is easy to verify. We can check the phase portrait given in Figure 2.

Proposition 2.2. *The 2D system (4) has no closed orbit around E_M in the first quadrant, and the equilibrium $E_M = (A_M^*, S_M^*)$ is globally stable. Further, the set $\{(A, S) \,|\, 0 \le A \le A_M,\ 0 \le S \le S_M\}$ is a global attractor of the 2D system (4).*

Proof. Based on the phase portrait, given after the Proposition 1, there is no closed orbit around E_M. Then by Poincare-Bendixion Theorem and Proposition 1, the equilibrium $E_M = (A_M^*, S_M^*)$ is globally stable. Thus, the set $\{(A, S) \,|\, 0 \le A \le A_M,\ 0 \le S \le S_M\}$ is a global attractor of the 2D system. □

2.2 Properties of Adult trees, seedlings and herbivore system

Theorem 2.1. *The set $\Phi = \{(A, S, H) \,|\, 0 \le A \le A_M, 0 \le S \le S_M, 0 \le H \le M\}$ is a global attractor and therefore, it is positively invariant under the 3D system (1), where $A_M = \frac{r}{\gamma}(1 + \frac{p}{r})$, $S_M = \frac{p}{b}\frac{r}{\gamma}(1 + \frac{p}{r})$ and $M = \frac{\beta p A_M}{min\{b,\mu\}}$.*

To show Theorem 2.1, it is easy to check the positive cone is positively invariant firstly, then we only need to show the upper bound for each dimension. Two lemmas are given on the upper bounds of the system (1).

Lemma 2.1. *For all nonnegative initial condition* (A_0, S_0, H_0)*, the first two dimensions* $(A(t), S(t))$ *of the three dimensional system (1) eventually go to inside of the square* $[0, A_M] \times [0, S_M]$.

This can be easily shown by checking the phase portrait of the two dimensional system without herbivores, and we can see the direction of flow along the edges of the square region $[0, A_M] \times [0, S_M]$ is inward (refer to the Figure 2). Then the solution of the 2D system (4) without Herbivores $A(t)$, $S(t)$ are the upper solutions of the first two dimensions of 3D system (1), then $(A(t), S(t))$ of the three dimensional system eventually enters $[0, A_M] \times [0, S_M]$.

Lemma 2.2. *If the initial condition* (A_0, S_0, H_0) *is in the cube* $[0, A_M] \times [0, S_M] \times [0, +\infty]$*, then* $H(t)$ *is essentially bounded by* $M = \frac{\beta p A_M}{min\{b,\mu\}}$.

Proof. By Lemma 1, we know that $A(t) \leq A_M$, $S(t) \leq S_M$ for large t. Next, show $H(t)$ is bounded by M eventually.

Consider $V = \beta S(t) + H(t)$. Then

$$\begin{aligned} \frac{dV(t)}{dt} &= \beta\frac{dS(t)}{dt} + \frac{dH(t)}{dt}, \\ &= \beta(pA - bS - C(S)H) + (\beta C(S)H - \mu H), \\ &= \beta pA - \beta bS - \mu H, \\ &\leq \beta pA_K - min\{b, \mu\}V, \end{aligned}$$

and this implies $V(t) \leq M = \frac{\beta p A_M}{min\{b,\mu\}}$ for all large t. Thus, $H(t) \leq V(t) <= M$ for all large t. ☐

Lemma 1 and Lemma 2 implies Theorem 1. For any nonnegative initial value (A_0, S_0, H_0), the solution $(A(t), S(t), H(t))$ of the 3D system eventually goes to the the set Φ. It is easy to check that all biological feasible equilibria have to be in Φ. Therefore, we can focus on the set $\Phi = \{(A, S, H) \,|\, 0 \leq A \leq A_M, 0 \leq S \leq S_M, 0 \leq H \leq M\}$.

3 Stability analysis of equilibria and bifurcations

To investigate the more complicated dynamical behaviors as mentioned in section 1, we confine $G \in [1/4h, 1/2h]$, where the toxin-determined functional response $C(S)$ is unimodal.

3.1 Equilibria

To find the equilibria of the 3D system $E^* = (A^*, S^*, H^*)$, we need to solve the following equations,

$$\begin{aligned} rA^* - \gamma A^{*2} + bS^* &= 0, & (5) \\ pA^* - bS^* - C(S^*)H^* &= 0, & (6) \\ \beta C(S^*)H^* - \mu H^* &= 0. & (7) \end{aligned}$$

The last equation can be written as $H^*(\beta C(S^*) - \mu) = 0$, which implies either $H^* = 0$ or $C(S^*) = \mu/\beta$. When $H^* = 0$, we can find two boundary equilibiria $E_1 = (0, 0, 0)$ and $E_M = (A_M, S_M, 0)$, which always exist.

As for interior equilibrium points, we have $C(S^*) = \mu/\beta$, we can rewrite the equation as in [17]

$$c_2S^2 + c_1S + c_0 = 0, \tag{8}$$

where

$$c_0 = -\mu G, \quad c_1 = e\sigma(\beta - 2\mu h)G, \quad c_2 = (\beta hG - \beta/4 - \mu h^2G)(e\sigma)^2$$

The discriminant of (8) is $\Delta_S = (e\sigma)^2\beta G(\beta G - \mu)$, the equation (8) has real roots if only if $\mu \leq \beta G$, which determines a threshold line

$$\bar{\mu}(G) = \beta G \tag{9}$$

The number of real solutions to (8) is determined by (9), i.e. given $c_2 \neq 0$, (8) has two (one, or zero) real roots if only if $\mu < \bar{\mu}(G)$ ($\mu = \bar{\mu}(G)$, or $\mu > \bar{\mu}(G)$). We consider the same region as in [17]

$$\Omega = \{(G, d) \,|\, \frac{1}{4h} < G < \frac{1}{2h},\ 0 \leq \mu \leq \bar{\mu}(G)\}.$$

Denote the two real solutions to (8)

$$S_1^* = \frac{e\sigma(2\mu h - \beta)G - \sqrt{\Delta_S}}{(\beta hG - \beta/4 - \mu h^2 G)(e\sigma)^2}, \; S_2^* = \frac{e\sigma(2\mu h - \beta)G + \sqrt{\Delta_S}}{(\beta hG - \beta/4 - \mu h^2 G)(e\sigma)^2}.$$

Then

$$A_i^* = \frac{r + \sqrt{r^2 + 4\gamma b S_i^*}}{2\gamma} \left(\geq \frac{r}{\gamma} \right), \; i = 1, 2, \tag{10}$$

and

$$\begin{aligned} H_i^* &= \frac{\beta}{\mu}((p+r)A_i^* - \gamma A_i^{*2}), \\ &= \frac{r - 2\gamma b S_i^* + \sqrt{r^2 + 4\gamma b S_i^*}}{2\gamma C(S_i^*)} \; i = 1, 2. \end{aligned} \tag{11}$$

The relation of S_M and S_m also will affect the number of interior equilibria in Φ, where $S_m = \frac{2G}{e\sigma(1-2Gh)}$ and the functional response $C(S)$ reaches the maximum G at S_m. It is easy to see that

$$S_m < (= \text{or} >)\, S_M \text{ if only if } G < (= \text{or} >)\, G_c,$$

where

$$G_c = \frac{e\sigma S_M}{2(1 + he\sigma S_M)} = \frac{e\sigma A_M}{2(\frac{b}{p} + he\sigma A_M)}$$

It is clear that $G_c < \frac{1}{2h}$, and we can verify that

$$G_c > \frac{1}{4h} \text{ if only if } A_M > \frac{b}{phe\sigma} \left(S_M > \frac{1}{he\sigma} \right).$$

This condition is true if A_M is sufficiently large, which is easy to satisfy. Remember that (A_M, S_M) is the global attractive node of the 2D system (4), which are the biomass of adult trees and the biomass of seedlings without herbivores.

In case of $G < G_c$, then $S_m < S_M$. It is easy to see that E_1^* always exists in Φ, E_2^* exists if $S_2^* < S_M$, which implies $S_2^* = S_M$ is a threshold. It is equivalent to $C(S_M) = \mu/\beta$, or

$$\mu_M(G) = \frac{\beta e\sigma S_M(4G(1 + he\sigma S_M) - e\sigma S_M)}{4G(1 + he\sigma S_M)^2}.$$

So we see $S_2^* < S_M$ if only if $\mu > \mu_M(G)$. Thus, both interior equilibria E_1^* and E_2^* exist for $\mu > \mu_M(G)$, or else only E_1^* exists for $\mu < \mu_M(G)$.

In the other case, $G > G_c$, then $S_m > S_M$. Notice $C(S)$ is monotone on

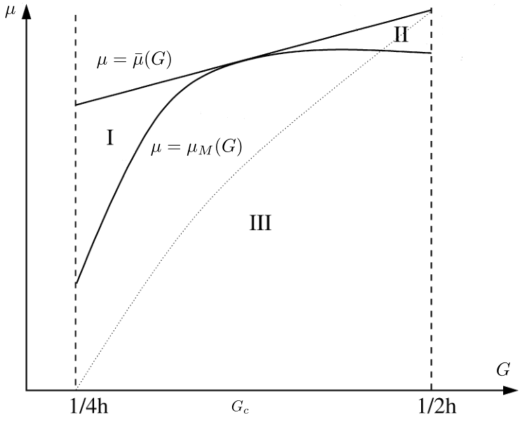
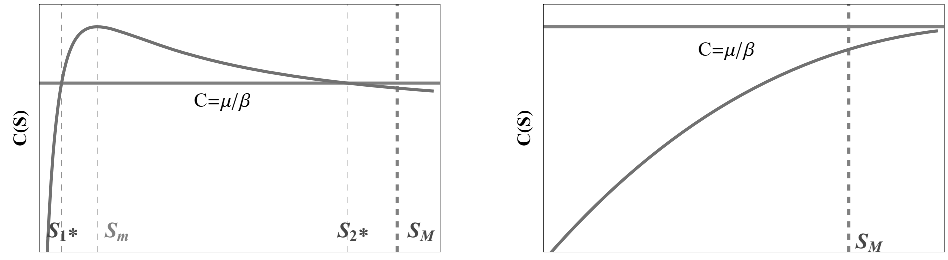


Figure 3: This graph shows the relation between $\mu = \bar{\mu}(G)$ and $\mu = \mu_M(G)$. They intersect at $G = G_c$ and $\mu = \beta G_c$. The two curves divide the region Ω into 3 subregions. In region I, there are two interior equilibria E_1^* and E_2^*. In region II, no interior equilibrium exists. In region III, there exist only E_1^* and region III can be divided into two piece by $G = G_c$. There are four possible cases on the existence of interior equilibria shown in Figure 4. The graph is modified from Figure 4 in [17].

$[0, S_M]$. There exists only one interior equilibrium E_1^* if $\mu < \mu_M(G)$. There is no interior equilbrium if $\mu > \mu_M(G)$.

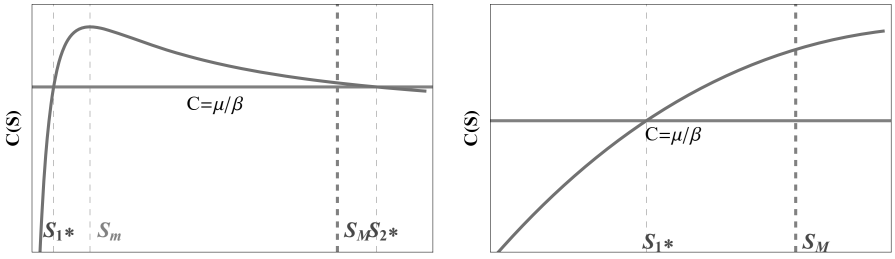
The curve $\mu = \bar{\mu}(G)$ and the curve $\mu = \mu_M(G)$ have the relation as shown in Figure 3, which is adapted from Figure 4 of [17]. They are monotonically increasing, $\mu_M(G) < \bar{\mu}(G)$ for $\frac{1}{4h} < G < \frac{1}{2h}$, and intersect at $G = G_c$. Figure 4 discribes the four possible cases of the existence of interior equilibria. The remark of [17] on the threshold generated by $c_2 = 0$ also applies here. The $c_2 = 0$ curve (the dashed curve int Figure 3) does not affect the number or stability of interior equilibria.

Based on the discussion, there is a saddle-node bifurcation curve, $\mu = \beta G$ on $1/4h < G < G_c$. As parameters μ and G cross the curve, the number of interior equilibrium points varies from zero ($\mu > \beta G$) to one ($\mu = \beta G$) to two ($\mu < \beta G$).



(a) Region I, two roots

(b) Region II, no root



(c) Region III, $G < G_c$, one root

(d) Region III, $G > G_c$, one root

Figure 4: The existence of interior equilibrium points based on $C(S) = \mu/\beta$. Fig (a) shows two roots as (G, μ) in Region I of Figure 3. Fig (b) shows no root as (G, μ) in Region II of Figure 3. Fig (c) shows one biological feasible root as (G, μ) in Region III of Figure 3 when $G < G_c$. Fig (d) shows one root as (G, μ) in Region III of Figure 3 when $G > G_c$.

3.2 Local stability of equilbria and Hopf bifurcation

The Jacobian matrix at equilibria $E^* = (A^*, S^*, H^*)$ is

$$J_{E^*} = \begin{pmatrix} r - 2\gamma A^* & b & 0 \\ p & -b - C'(S^*)H^* & -C(S^*) \\ 0 & \beta C'(S^*)H^* & \beta C(S^*) - \mu \end{pmatrix}. \tag{12}$$

3.2.1 Boundary equilibria

At $E_0 = (0, 0, 0)$, the Jacobian matrix is

$$J_{E_0} = \begin{pmatrix} r & b & 0 \\ p & -b & 0 \\ 0 & 0 & -\mu \end{pmatrix}. \tag{13}$$

Clearly, J_{E_0} has a negative eigenvalue, $\lambda_3 = -\mu$, and the submatrix

$$\hat{J} = \begin{pmatrix} r & b \\ p & -b \end{pmatrix}. \tag{14}$$

has $det(\hat{J}) = \lambda_1\lambda_2 = -rb - bp < 0$, which implies $\hat{J}$ has a positive eigenvalue and a negative eigenvalue. So J_{E_0} has a positive eigenvalue and two negative eigenvalues. Hence E_0 is always unstable.

At $E_M = (A_M, S_M, 0) = ((r/\gamma)(1 + p/r), (pr/b\gamma)(1 + p/r), 0)$, the Jacobian matrix is

$$J_{E_M} = \begin{pmatrix} r - 2\gamma A_M & b & 0 \\ p & -b & -C(S_M) \\ 0 & 0 & \beta C(S_M) - \mu \end{pmatrix}. \tag{15}$$

It has an eigenvalue $\lambda_3 = \beta C(S_M) - \mu$, and the other two eigenvalues λ_1, λ_2 are also the eigenvalues of the submatrix

$$\tilde{J} = \begin{pmatrix} r - 2\gamma A_M & b \\ p & -b \end{pmatrix}. \tag{16}$$

The trace of $\tilde{J}$ is

$$tr(\tilde{J}) = \lambda_1 + \lambda_2 = (r - 2\gamma A_M) - b = -r - 2p < 0,$$

and the determinant of $\tilde{J}$ is

$$det(\tilde{J}) = \lambda_1\lambda_2 = (r - 2\gamma A_M)(-b) - bp = b(r + p) > 0.$$

and the discriminant is

$$\Delta = tr^2(\tilde{J}) - 4det(\tilde{J}) = (-r - 2p - b)^2 - 4b(r + p) = (r - b)^2 + 4p(p + r) > 0.$$

Thus, $\lambda_1, \lambda_2 < 0$, and if $\lambda_3 = \beta C(S_M) - \mu < 0$ then E_M is stable, or if $\lambda_3 = \beta C(S_M) - \mu > 0$ then E_M is unstable. Referring to Figure 3 and Figure 4, we have the following result.

Proposition 3.1. *The boundary equilibrium E_0 is always unstable. The other boundary equilibrium E_M is stable if $G < G_c$ and $\mu > \mu_M(G)$, i.e. (G, μ) in Region I, or $G > G_c$ and $\mu > \mu_M(G)$, i.e. (G, μ) in Region II, and E_M is unstable if $\mu < \mu_M(G)$, i.e. (G, μ) in Region III.*

3.2.2 Interior equilibria and Hopf bifurcation

At $E_i^* = (A_i^*, S_i^*, H_i^*)$, $i = 1, 2$, the Jacobian matrix is

$$J_{E_i^*} = \begin{pmatrix} r - 2\gamma A_i^* & b & 0 \\ p & -b - C'(S_i^*)H_i^* & -\mu/\beta \\ 0 & \beta C'(S_i^*)H_i^* & 0 \end{pmatrix}. \tag{17}$$

The determinant of $J_{E_i^*}$ is

$$det(J_{E_i^*}) = \lambda_1\lambda_2\lambda_3 = -(r-2\gamma A_i^*)(-\frac{\mu}{\beta})\beta C'(S_i^*)H_i^* = -\sqrt{r^2 + 4\gamma b S_i^*}\mu C'(S_i^*)H_i^*.$$

Recalling $C(S)$ is unimodal, $C'(S_1^*) > 0$ and $C'(S_2^*) < 0$ imply that $det(J_{E_1^*}) < 0$ and $det(J_{E_2^*}) > 0$. Thus, $J_{E_2^*}$ has at least a positive eigenvalue. Thus, it is unstable.

Proposition 3.2. *If the equilibrium of E_2^* exists, i.e. (G, μ) in Region I, then it has to be unstable.*

However, $J_{E_1^*}$ could have all negative real eigenvalues, a negative real eigenvalue with two positive real eigenvalues, or a negative real eigenvalue with a pair of complex eigenvalues. It means E_1^* could be a stable node, or unstable node, or stable/unstable focus. The stability of E_1^* needs further investigation.

At E_1^*, the characteristic matrix is

$$\lambda I - J_{E_1^*} = \begin{pmatrix} \lambda - (r - 2\gamma A_1^*) & -b & 0 \\ -p & \lambda + (b + C'(S_1^*)H_1^*) & \mu/\beta \\ 0 & -\beta C'(S_1^*)H_1^* & \lambda \end{pmatrix},$$

we can calculate the determinant of the characteristic matrix, which gives us characteristic equation

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{18}$$

where

$$\begin{aligned} a_1 &= (2\gamma A_1^* - r) + (b + C'(S_1^*)H_1^*), \\ a_2 &= (2\gamma A_1^* - r)(b + C'(S_1^*)H_1^*) + \mu C'(S_1^*)H_1^* - pb, \\ a_3 &= (2\gamma A_1^* - r)\mu C'(S_1^*)H_1^*. \end{aligned}$$

Denote

$$\begin{aligned} &a_{11} = (2\gamma A_1^* - r) = \sqrt{r^2 + 4\gamma b S_1^*}, \\ &a_{12} = b + C'(S_1^*)H_1^* = b + \frac{C'(S_1^*)}{2\gamma C(S_1^*)}(r - 2\gamma b S_1^* + \sqrt{r^2 + 4\gamma b S_1^*}), \\ &a_{22} = \mu C'(S_1^*)H_1^* = \frac{\beta}{2\gamma}C'(S_1^*)(r - 2\gamma b S_1^* + \sqrt{r^2 + 4\gamma b S_1^*}), \\ &a_{23} = pb, \end{aligned}$$

then it is easy to check a_{11}, a_{12}, a_{22}, $a_{23} > 0$, and

$$a_1 = a_{11} + a_{12}, \ a_2 = a_{11}a_{12} + a_{22} - a_{23}, \ a_3 = a_{11}a_{22}.$$

It is easy to see $a_1 > 0$, $a_3 > 0$, and by Routh-Hurwitz Criterion ($a_1 > 0$, $a_3 > 0$, $a_1a_2 > a_3$ if only if the real parts of the eigenvalues are negative), if $a_1a_2 - a_3 > 0$, and then E_1^* is stable. If $a_1a_2 - a_3 < 0$, E_1^* is unstable. Thus, we can summarize the linear stability result in the Table 1.

Further, we investigate more on the condition for the stability of equilibrium E_1^*. Based on

$$\begin{aligned} a_1a_2 - a_3 &= (a_{11} + a_{12})(a_{11}a_{12} + a_{22} - a_{23}) - a_{11}a_{22}, \\ &= a_{11}(a_{11}a_{12} - a_{23}) + a_{12}(a_{11}a_{12} + a_{22} - a_{23}), \end{aligned}$$

Equilibrium	Region I	Region II	Region III
E_0	unstable	unstable	unstable
E_M	stable	stable	unstable
E_1^*	stable if $a_1a_2 - a_3 > 0$ unstable if $a_1a_2 - a_3 < 0$	does not exist	stable if $a_1a_2 - a_3 > 0$ unstable if $a_1a_2 - a_3 < 0$
E_2^*	unstable	does not exist	does not exist

Table 1: Linear stability of equilibria of the system (1). Refer to Figure 3 for the parameter regions.

one simple sufficient condition is $a_{11}a_{12} - a_{23} > 0$, which is

$$\begin{aligned} a_{11}a_{12} - a_{23} &= (2\gamma A_1^* - r)(b + C'(S_1^*)H_1^*) - pb, \\ &\geq (\sqrt{r^2 + 4\gamma b S_1^*} - p)b > 0, \end{aligned}$$

if $S_1^* > \frac{1}{4\gamma b}(p^2 - r^2) \triangleq S_b$, equivalently, $\mu > \beta C(S_b)$ when $p > r$, or when $p < r$, define $S_b = 0$ and it is true for any $S_1^* > 0$, $0 < \mu < \bar{\mu}(G)$.

Notice when $p > r$, there is no $S_1^* > S_b$ if $S_b > S_m$. Thus, we need $S_b < S_m$, and notice

$$S_b = \frac{1}{4\gamma b}(p^2 - r^2) < \frac{2G}{e\sigma(1 - 2Gh)} = S_m$$

which is equivalent to $G > G_b$, where

$$G_b = \frac{1}{2}\frac{e\sigma\frac{(p^2-r^2)}{4\gamma b}}{1 + he\sigma\frac{(p^2-r^2)}{4\gamma b}} = \frac{1}{2}f(\frac{p^2 - r^2}{4\gamma b}) = \frac{1}{2}f(S_b)$$

by recalling $f(S) = \frac{e\sigma S}{1+he\sigma S}$, and notice $0 < f(S) < \frac{1}{h}$, then $G_b < \frac{1}{2h}$. If γ is small enough, biologically equivalently, A_M and S_M are large, then $f(S_b) > \frac{1}{2h}$, and $\frac{1}{4h} < G_b < \frac{1}{2h}$. So we have shown the following proposition.

Proposition 3.3. *The interior equilibrium E_1^* is locally asymptotically stable, if $G > G_b$ and $\mu > \beta C(S_b)$, where $S_b = \frac{1}{4\gamma b}(p^2 - r^2)$ when $p > r$, or $S_b = 0$ when $p < r$, and $G_b = \frac{1}{2}f(S_b)$.*

Next, consider the case of $G < G_b$. We can view that a_1, a_2, a_3 as functions of S_1^* by replacing $\mu = \beta C(S_1^*)$, then varying μ is equivalent to varying S_1^*. It is easy to see that this is a 1-1 mapping, when $\mu = 0$, $S_1^* = 0$, and when $\mu = \bar{\mu}(G)$, $S_1^* = S_m$.

At $S_1^* = S_m$, it is easy to check that $(a_{11}a_{12} - a_{23})(S_m) < 0$, since

$$\begin{aligned} a_{11}a_{12} + a_{22} - a_{23} &= a_{11}a_{12} - a_{23}, \\ &= b(\sqrt{r^2 + 4\gamma b S_m} - p) < 0. \end{aligned}$$

This means when S_1^* is near S_m (or μ is near $\bar{\mu}(G)$), by Routh-Hurwitz Criterion, E_1^* is unstable.

On the other hand, as $S_1^* \to 0$, we see that $(a_{11}a_{12} - a_{23})(S_1^*) \to +\infty$, since

$$\begin{aligned} a_{11}a_{12} - a_{23} &= \sqrt{r^2 + 4\gamma b S_1^*}(b + \frac{C'(S_1^*)}{2\gamma C(S_1^*)}(r - 2\gamma b S_1^* + \sqrt{r^2 + 4\gamma b S_1^*})) - pb, \\ &\to r(b + (+\infty)) - pb > 0, \end{aligned}$$

where

$$\sqrt{r^2 + 4\gamma b S}$$

is increasing and is bounded on $[0, S_m)$, and

$$\frac{C'(S)}{C(S)} = \frac{1}{S}\frac{1}{1 + he\sigma S}(2 - \frac{1}{1 - \frac{1}{4G}f(S)})$$

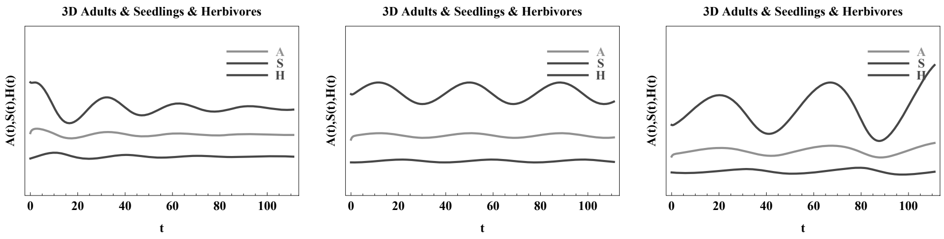
is a decreasing function of S, it approaches $+\infty$ at $S \to 0$ and it is zero at $S = S_m$, and

$$r - 2\gamma b S + \sqrt{r^2 + 4\gamma b S}$$

is increasing on $[0, (1 - r^2)/4\gamma b)$, decreasing on $((1 - r^2)/4\gamma b, S_m)$ and it is bounded on $(0, S_m)$. This means when S_1^* is small (or μ is near 0), by Routh-Hurwitz Criterion, E_1^* is stable.

The switch of stability of E_1^* implies the possibility of Hopf bifurcation. From the above argument, by Intermediate Theorem, there exists a $S_h \in (0, S_m)$, such that $(a_{11}a_{12} - a_{23})(S_h) = 0$. Combined with $a_1(S_h) > 0$, $J_{E_1^*}$ has one eigenvalue with negative real part and two eigenvalues with zero real part by the Theorem 1 of Yang [26]. By $a_3(S_h) > 0$ and $a_3(S_h) = -det(J_{E_1^*})$, there is no zero eigenvalues. Thus, we can conclude that $J_{E_1^*}$has one negative eigenvalue and a pair of pure complex eigenvalue.

Furthermore, if $\frac{\partial}{\partial S_1^*}(a_{11}a_{12} - a_{23})(S_h) \neq 0$, then there is a simple Hopf bifurcation by the Theorem of Liu [20], or by the Theorem 2 of Yang [26], if $\frac{\partial^i}{\partial (S_1^*)^i}(a_{11}a_{12} - a_{23})(S_h) = 0$ for $i = 1, \ldots j-1$, and $\frac{\partial^j}{\partial (S_1^*)^j}(a_{11}a_{12} - a_{23})(S_h) \neq 0$, then there is a j-order Hopf bifurcation. Due to the complication of computa-



(a) Stable focus (b) Periodic Solution (c) Unstable focus

Figure 5: Hopf Bifurcation. As μ increases, the stability of E_1^* switches from stable to unstable, and at some particular value, there bifucates a periodic solution.

tion of S_h and $\frac{\partial}{\partial S_1^*}(a_{11}a_{12}-a_{23})(S_1^*)$, we can not be sure that it is a simple Hopf bifurcation or a j-order Hopf bifurcation for some positive integer j. However, $(a_{11}a_{12}-a_{23})(S_1^*)$ crosses zero as S_1^* varies on $(0, S_m)$, and also by the composition of $(a_{11}a_{12}-a_{23})(S_1^*)$, it is impossible that its partial derivatives of all orders at S_h are zero. Thus, it has to be one of the two cases. Thus, we showed the following theorem.

Theorem 3.1. *In case of $G > G_b$, the equilibrium of E_1^* is unstable when μ is near $\bar{\mu}(G)$ and it is stable when μ is small. Furthermore, there exists a $\mu_h = \beta C(S_h)$, where S_h satisfies $(a_1a_2 - a_3)(S_h) = 0$, $S_h \in (0, S_m)$, such that a Hopf bifurcation occurs at $\mu = \mu_h$.*

Numerical simulation is conducted to show the periodic solution in Figure 5 when $r = 0.5$, $\gamma = 0.001$, $b = 0.1$, $p = 3.89$, $h = 0.1$, $e\sigma = 0.001$, $G = 3$, $\beta = 0.1$ and $\mu = 0.27$, $\mu = 0.28$ and $\mu = 0.285$, respectively.

3.3 The degenerated case of the interior equilibrium

At $G = G_b$ and $\mu = \beta G_b \triangleq \mu_b$, there is only one interior equilibrium E_m, where $E_m = (A_m, S_m, H_m)$. At E_m the Jacobian matrix is

$$J_{E_m} = \begin{pmatrix} -p & b & 0 \\ p & -b & -G \\ 0 & 0 & 0 \end{pmatrix}, \tag{19}$$

which has a negative eigenvalue $\lambda = -p - b$ and two zero eigenvalues. The Jacobian matrix has the Jordan Canonical Form

$$J = Q^{-1} J_{E_m} Q = \begin{pmatrix} -p-b & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}, \tag{20}$$

where

$$Q = \begin{pmatrix} \frac{Gp}{(p+b)^2} & -\frac{bG}{p+b} & \frac{Gb(2p+b)}{p(p+b)^2} \\ -\frac{Gp}{(p+b)^2} & -\frac{Gp}{p+b} & \frac{Gp}{(p+b)^2} \\ 0 & 0 & 1 \end{pmatrix}, \tag{21}$$

and

$$Q^{-1} = \begin{pmatrix} \frac{p+b}{G} & -\frac{b(p+b)}{Gp} & -\frac{b}{p} \\ -\frac{1}{G} & -\frac{1}{G} & \frac{1}{p} \\ 0 & 0 & 1 \end{pmatrix}. \tag{22}$$

This implies that the equilibrium E_m is a degenerated equilibrium, which may be a Bogdanov-Takens cusp of codimension 2, because (i) when $\mu = \beta G_b$ the two possible interior equilibria E_1^* and E_2^* merge to one interior equilibrium E_m, (ii) the condition of $G = G_b$ implies that $S_m = S_b$ and further $(a_1 a_2 - a_3)(S_m) = 0$, which is the condition of Hopf bifurcation. This can be proved in the theorem.

Theorem 3.2. *For $(G, \mu) = (G_b, \mu_b)$, where $\mu_b = \beta G_b$, the 3D system (1) has a Bogdanov-Takens cusp point of codimension 2 at $E_m = (A_m, S_m, H_m)$.*

Proof. To confirm the equilibrium E_m could be a Bogdanov-Takens cusp of codimension 2, we do the following transformations to convert the system to its normal form.

First, translate the equilibrium E_m to the origin by letting $x_1 = A - A_m$, $x_2 = S - S_m$, $x_3 = H - H_m$. Then the system can be written as

$$\begin{aligned} \dot{X} &= J_{E_m} X + F(X) + O(\|X\|^3), \\ &= \begin{pmatrix} -p & b & 0 \\ p & -b & -G \\ 0 & 0 & 0 \end{pmatrix} X + \begin{pmatrix} -\frac{r}{K} x_1^2 \\ -\frac{1}{2} H_m C''(S_m) x_2^2 \\ \frac{1}{2} \beta H_m C''(S_m) x_2^2 \end{pmatrix} + O(\|X\|^3), \end{aligned}$$

where $F(X)$ is second order terms.

Next, let $X = QY$, i.e.

$$
\begin{aligned}
X &= QY = \begin{pmatrix} \frac{Gp}{(p+b)^2} & -\frac{bG}{p+b} & \frac{Gb(2p+b)}{p(p+b)^2} \\ -\frac{Gp}{(p+b)^2} & -\frac{Gp}{p+b} & \frac{Gp}{(p+b)^2} \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \\ y_3 \end{pmatrix}, \\
&= \begin{pmatrix} \frac{Gp}{(p+b)^2} y_1 - \frac{bG}{p+b} y_2 + \frac{Gb(2p+b)}{p(p+b)^2} y_3 \\ -\frac{Gp}{(p+b)^2} y_1 - \frac{Gp}{p+b} y_2 + \frac{Gp}{(p+b)^2} y_3 \\ y_3 \end{pmatrix}, \\
&\triangleq \begin{pmatrix} q_{11}y_1 + q_{12}y_2 + q_{13}y_3 \\ q_{21}y_1 + q_{22}y_2 + q_{23}y_3 \\ y_3 \end{pmatrix}.
\end{aligned}
$$

Then substitute $X = QY$ and $Y = Q^{-1}X$, and we get

$$
\begin{aligned}
\dot{Y} &= (Q^{-1}J_{E_m}Q)Y + M(Y) + O(\|Y\|^3), \\
&= \begin{pmatrix} -p-b & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix} Y + \begin{pmatrix} m_{11}y_1^2 + m_{12}y_2^2 + m_{13}y_3^2 + m_{14}y_1y_2 + m_{15}y_1y_3 + m_{16}y_2y_3 \\ m_{21}y_1^2 + m_{22}y_2^2 + m_{23}y_3^2 + m_{24}y_1y_2 + m_{25}y_1y_3 + m_{26}y_2y_3 \\ m_{31}y_1^2 + m_{32}y_2^2 + m_{33}y_3^2 + m_{34}y_1y_2 + m_{35}y_1y_3 + m_{36}y_2y_3 \end{pmatrix} \\
&\quad + O(\|Y\|^3),
\end{aligned}
$$

where $M(Y) = Q^{-1}F(X) = Q^{-1}F(QY)$, and

$$
\begin{aligned}
Q^{-1}F(X) &= \begin{pmatrix} \frac{p+b}{G} & -\frac{b(p+b)}{Gp} & -\frac{b}{p} \\ -\frac{1}{G} & -\frac{1}{G} & \frac{1}{p} \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} -\frac{r}{K}x_1^2 \\ -\frac{1}{2}H_mC''(S_m)x_2^2 \\ \frac{1}{2}\beta H_mC''(S_m)x_2^2 \end{pmatrix}, \\
&= \begin{pmatrix} -\frac{(p+b)r}{GK}x_1^2 + \frac{1}{2}\left(\frac{b(p+b)H_mC''(S_m)}{Gp} - \frac{b\beta H_mC''(S_m)}{p}\right)x_2^2 \\ \frac{r}{GK}x_1^2 + \frac{1}{2}\left(\frac{H_mC''(S_m)}{G} + \frac{\beta H_mC''(S_m)}{p}\right)x_2^2 \\ \frac{1}{2}\beta H_mC''(S_m)x_2^2 \end{pmatrix}, \\
&\triangleq \begin{pmatrix} l_{11}x_1^2 + l_{12}x_2^2 \\ l_{21}x_1^2 + l_{22}x_2^2 \\ l_{31}x_2^2 \end{pmatrix},
\end{aligned}
$$

$$\begin{aligned}
M(Y) &= Q^{-1}F(X) = Q^{-1}F(QY), \\
&= \begin{pmatrix} l_{11}(q_{11}y_1 + q_{12}y_2 + q_{13}y_3)^2 + l_{12}(q_{21}y_1 + q_{22}y_2 + q_{23}y_3)^2 \\ l_{21}(q_{11}y_1 + q_{12}y_2 + q_{13}y_3)^2 + l_{22}(q_{21}y_1 + q_{22}y_2 + q_{23}y_3)^2 \\ l_{31}(q_{21}y_1 + q_{22}y_2 + q_{23}y_3)^2 \end{pmatrix}, \\
&\triangleq \begin{pmatrix} m_{11}y_1^2 + m_{12}y_2^2 + m_{13}y_3^2 + m_{14}y_1y_2 + m_{15}y_1y_3 + m_{16}y_2y_3 \\ m_{21}y_1^2 + m_{22}y_2^2 + m_{23}y_3^2 + m_{24}y_1y_2 + m_{25}y_1y_3 + m_{26}y_2y_3 \\ m_{31}y_1^2 + m_{32}y_2^2 + m_{33}y_3^2 + m_{34}y_1y_2 + m_{35}y_1y_3 + m_{36}y_2y_3 \end{pmatrix}.
\end{aligned}$$

Further, use Center Manifold Theorem to reduce the system to its 2D center manifold, $W^C(0) = \{(y_1, (y_2, y_3)) \in R^s \times R^c \mid y_1 = h(y_2, y_3)\}$, when (y_1, y_2, y_3) is in a small neighborhood of the equilibrium, where $h(0, 0) = 0$ and $Dh(0, 0) = 0$, since h passes through the origin and is tangent to invariant subspace. Thus, $h(y_2, y_3)$ consists of second or higher order terms of (y_2, y_3). The system can be written as $\dot{y}_1 = \lambda y_1 + G(y_1, z)$, and $\dot{z} = Cz + F(y_1, z)$, where $z = (y_2, y_3)$.

Let $h(z) = h(y_2, y_3) = ay_2^2 + by_2y_3 + cy_3^2 + \cdots$, then $Dh(y_2, y_3) = [2ay_2 + by_3 + \cdots,\ by_2 + 2cy_3 + \cdots]$. Then we differentiate both sides of $y_1 = h(z) = h(y_2, y_3)$ and substitute the derivatives from the system in and we get $\lambda h(z) + G(h(z), z) = Dh(z)(Cz + F(h(z), z))$. By comparing the coefficients of the same order terms, we can determine the coefficients in $h(y_2, y_3)$. Compute

$$\begin{aligned}
& Dh(y_2, y_3)[\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}\begin{pmatrix} y_2 \\ y_3 \end{pmatrix} \\
+ & \left(\begin{matrix} m_{21}(ay_2^2 + by_2y_3 + cy_3^2)^2 + m_{22}y_2^2 + m_{23}y_3^2 + m_{24}(ay_2^2 + by_2y_3 + cy_3^2)y_2 \\ m_{31}(ay_2^2 + by_2y_3 + cy_3^2)^2 + m_{32}y_2^2 + m_{33}y_3^2 + m_{34}(ay_2^2 + by_2y_3 + cy_3^2)y_2 \end{matrix}\right. \\
& \left.\begin{matrix} +m_{25}(ay_2^2 + by_2y_3 + cy_3^2 + \cdots)y_3 + m_{26}y_2y_3 \\ +m_{35}(ay_2^2 + by_2y_3 + cy_3^2 + \cdots)y_3 + m_{36}y_2y_3 \end{matrix}\right) + \cdots \\
= & \ 2ay_2y_3 + by_3^2 + \cdots ,
\end{aligned}$$

and

$$\begin{aligned}
& \lambda h(y_2, y_3) + (m_{11}(ay_2^2 + by_2y_3 + cy_3^2)^2 + m_{12}y_2^2 + m_{13}y_3^2 \\
& +m_{14}(ay_2^2 + by_2y_3 + cy_3^2)y_2 + m_{15}(ay_2^2 + by_2y_3 + cy_3^2 + \cdots)y_3 + m_{16}y_2y_3) \\
= & \ (\lambda a + m_{12})y_2^2 + (\lambda b + m_{16})y_2y_3 + (\lambda c + m_{13}) + \cdots .
\end{aligned}$$

Comparing the above two equations, the coefficient of y_2^2 implies $0 = \lambda a + m_{12}$, the coefficient of y_2y_3 implies $2a = \lambda b + m_{16}$, and the coefficient of y_3^2 implies

$b = \lambda c + m_{13}$, where $\lambda = -p - b$ is the negative eigenvalue. Solving for a, b, c, we get

$$\begin{aligned} a &= -\frac{1}{\lambda} m_{12}, \\ b &= -\frac{2}{\lambda^2} m_{12} - \frac{1}{\lambda} m_{16}, \\ c &= -\frac{2}{\lambda^3} m_{12} - \frac{1}{\lambda^2} m_{16} - \frac{1}{\lambda} m_{13}, \end{aligned}$$

and

$$y_1 = h(y_2, y_3) = -\frac{1}{\lambda} m_{12} y_2^2 - (\frac{2}{\lambda^2} m_{12} + \frac{1}{\lambda} m_{16}) y_2 y_3 - (\frac{2}{\lambda^3} m_{12} + \frac{1}{\lambda^2} m_{16} + \frac{1}{\lambda} m_{13}) y_3^2. \tag{23}$$

On the center manifold $W^C(0)$, noticing that all terms containing y_1 become higher order terms after plugging $y_1 = h(y_1, y_2)$, we have reduced the 3D system to 2D system as

$$\begin{pmatrix} \dot{y_2} \\ \dot{y_3} \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} y_2 \\ y_3 \end{pmatrix} + \begin{pmatrix} m_{22} y_2^2 + m_{23} y_3^2 + m_{26} y_2 y_3 \\ m_{32} y_2^2 + m_{33} y_3^2 + m_{36} y_2 y_3 \end{pmatrix} + O(\|Y\|^3).$$

By Remark 1 on Page 166 and Problem 1 on Page 167 of Perko's Book, under a near-identity transformation,

$$u = y_2 + \frac{1}{2}(m_{26} + m_{33}) y_2^2, \; v = y_3 - m_{22} y_2^2 + m_{33} y_2 y_3 - m_{23} y_3^2,$$

the 2D system can be reduced to the normal form

$$\begin{aligned} \dot{u} &= v \\ \dot{v} &= m_{32} u^2 + (m_{36} + 2 m_{22}) uv + O(\|(u, v)\|^3) \end{aligned}$$

We can verify the coefficients $m_{32} \neq 0$ and $(m_{36} + 2m_{22}) \neq 0$, thus the equilibrium is a cusp. Noticing that $C''(S_m) < 0$, then

$$m_{32} = l_{32} q_{22}^2 = \frac{1}{2} \beta H_m C''(S_m) (-\frac{Gp}{p+b})^2 < 0, \tag{24}$$

and

$$\begin{aligned} m_{36} &= l_{31}(2q_{22}q_{23}) = \frac{1}{2}\beta H_m C''(S_m)(-\frac{Gp}{p+b})(\frac{Gp}{(p+b)^2}), \\ &= -\beta H_m C''(S_m)\frac{(Gp)^2}{(p+b)^3} > 0, \\ m_{22} &= l_{21}q_{12}^2 + l_{22}q_{22}^2, \\ &= (\frac{\gamma}{G})(-\frac{bG}{p+b})^2 + \frac{1}{2}(\frac{H_m C''(S_m)}{G} + \frac{\beta H_m C''(S_m)}{p})(-\frac{Gp}{p+b})^2, \\ &= (\frac{\gamma}{G})(\frac{bG}{p+b})^2 + \frac{1}{2}(\frac{H_m C''(S_m)}{G} + \frac{\beta H_m C''(S_m)}{p})(\frac{Gp}{p+b})^2, \\ &= (positive) + (negative), \end{aligned}$$

so

$$\begin{aligned} m_{36} + 2m_{22} &= -\beta H_m C''(S_m)\frac{(Gp)^2}{(p+b)^3} + \frac{2\gamma}{G}(\frac{bG}{p+b})^2 + (\frac{H_m C''(S_m)}{G} + \frac{\beta H_m C''(S_m)}{p})(\frac{Gp}{p+b})^2, \\ &= \frac{2\gamma}{G}(\frac{bG}{p+b})^2 + \beta H_m C''(S_m)(\frac{Gp}{p+b})^2(-\frac{1}{p+b} + \frac{1}{p}) + \frac{H_m C''(S_m)}{G}(\frac{Gp}{p+b})^2, \\ &= (positive) + (negative) + (negative) \neq 0, \end{aligned}$$

if

$$\frac{1}{\gamma} \neq \frac{2b^2(p+b)}{p(\beta Gb + p^2 + bp)H_m(-C''(S_m))},$$

so if γ is small, then the equilibrium is a cusp of codimension 2. Thus, we have proved the theorem. □

4 Conclusion and future work

In this paper, we formulated a three dimensional ordinary differential equations model to describe the interaction of plant-herbivores with size structure in plants. Our model includes two plant compartments, for adult plants and seedlings respectively, and one herbivore population. The plant structure is modeled explicitly with the effect of plant toxin jointly to study the interaction of plants and herbivores, which has not been studied before in this way.

We validated the model and gave an global attractor of the model. Then we investigated the rich dynamics of this model, including the stability of equilibria and bifurcation analysis. The plant toxin measurement G and herbivore health measurement μ were used as bifurcation parameters and varied in biological ranges. A saddle-node bifurcation and a Hopf bifurcation were shown analytically. Furthermore, there is a Bogdanov-Takens cusp of codimension 2 identified at (G_b, μ_b). Thus, besides the Hopf bifurcation and the saddle-node bifurcation, there is a homoclinic bifurcation as G and μ vary in the neighborhood of (G_b, μ_b). The dynamics of this model exhibits the complex dynamics similar to the two dimensional model studied in [17]. But the mathematical approach of this paper is different from [17] because of the difficulty of the analysis of high dimensional system. Hopf bifurcation theorems based on Routh-Hurwitz criterion were used to show the bifurcating limit cycle. The center manifold theorem was used to reduce the system to center manifold to study the degenerated equilibrium with one negative eigenvalue and two zero eigenvalues. Then normal form theory was employed to show the codimension 2 Bogdanov-Takens cusp.

To achieve full understanding the model, we would like to further to investigate the universal unfolding of the Bogdanov-Takens cusp to determine the bifurcation curves for the homoclinic bifurcation. Moreover, this model and the analysis done in this paper also serves as a preliminary step for the further research on the spatial dispersal process of the seedlings and herbivores when more space is available in the northern Alaska in the global warming process. The setup and analysis of a reaction-diffusion model is of mathematical and biological interests and will be our future study.

5 Acknowledgments

We would like to thank Dr. Carlos Castillo-Chavez, Executive Director of the Mathematical and Theoretical Biology Institute (MTBI), for giving us the opportunity to participate in this research program. We would also like to thank Co-Executive Summer Directors Dr. Erika T. Camacho and Dr. Stephen Wirkus for their efforts in planning and executing the day to day activities of MTBI. We also want to thank Professor Donald DeAngelis, Professor Wenzhang Huang and Professor John Bryant for the beneficial discussion on this topic. We also want to give special thanks to Professor Baojun Song, Professor Jose Flores and Romarie Morales for valuable discussion and comments at MTBI. This research was conducted in MTBI at the Mathematical, Computational and Modeling Sciences Center (MCMSC) at Arizona State University (ASU). This project has been partially supported by grants from the National Science Foundation (NSF grant DMS-0920828, NSF - Grant DMPS-1263374), the National Security Agency (NSA - Grant H98230-13-1-0261), the Office of the President of ASU, and the Office of the Provost of ASU.

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