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DYNAMICS OF A PLANT-HERBIVORE MODEL WITH TOXIN-INDUCED FUNCTIONAL RESPONSE

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Dedicated to Professor Horst R. Thieme on the Occasion of his 60th Birthday

Abstract. Traditional functional responses for plant-herbivore interactions do not take into account explicitly the effect of plant toxin. However, considerable evidence suggests that toxins set upper limits on food intake for many species of herbivorous vertebrates. In this paper, a mathematical model for plant-herbivore interactions mediated by toxin-determined functional response is studied. The model consists of three ordinary differential equations describing one herbivore population and two plant species with different toxicity levels. The effect of plant toxicity on herbivore's intake rate is incorporated explicitly in the model by assuming an increased handling time. The dynamical behaviors of the model are analyzed and the results are used to examine the influence of toxin-determined intake in the community composition of plant species. The bifurcation analysis presented in this paper suggests that the toxin-mediated functional response may have dramatic effects on plant-herbivore interactions.

1. **Introduction.** Over the past two decades, ecologists have focused intensively on chemically mediated plant-herbivore interactions [5, 10, 13, 18], and suggested that plant toxins play an important role in regulating herbivore's consumption of the plant [11, 12, 17, 18, 19]. Specific examples and more detailed discussions about the importance of plant toxins as determinants of herbivore functional response can be found in [16]. Although the impact of toxins on herbivores' diet has been emphasized in a great deal of research, it is frequently ignored in plant-herbivore models (e.g., [1, 8, 9, 15]). In [6], we constructed a toxin-determined functional response model (referred to as TDRFM) that explicitly incorporates the effect of

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toxicity on herbivore browsing. More specifically, in the case of a single plant species with density N, the toxin-determined functional response $C(N)$ has the form

$$C(N) = f(N)\Big(1 - \frac{\alpha f(N)}{G}\Big). \tag{1}$$

The function $f(N)$ is the Holling Type 2 functional response given by

$$f(N) = \frac{eN}{1 + heN}, \tag{2}$$

where e is the rate of encounter per unit of plant and h is the handling time per unit of plant in the absence of toxin. G is the toxin-adjusted maximal amount of plant an herbivore can ingest per unit time. It is assumed that $G < 1/h$ as $1/h$ is the maximum intake rate in the absence of toxins. The constraint $0 \le C(N) \le G$ requires that $\alpha = 1/4$ and $1/(4h) \le G \le 1/h$. In the functional response $C(N)$, the reduction of consumption due to toxins is modeled with the factor $1 - f(N)/(4G)$, which is between 0 and 1. The quantity $f(N)/(4G)$ represents a measure of how fast the herbivore is taking up a toxicant compared to the maximal rate of uptake that it can tolerate, which determines how much the maximal consumption is reduced due to toxicity.

The model studied in [6] is a three-dimensional system of ordinary differential equations with one herbivore population and two plant species, N_1 and N_2. The herbivore's functional response to the density of plant species i ($i = 1, 2$) is described by $C_i(N_1, N_2)$, which is an extension of $C(N)$ given in (1). The system exhibits much more complex dynamical behaviors than a similar system in which the Holling type 2 response is used. For the model studied in [6], due to the high nonlinearity introduced by the toxin-determined response $C_i(N_1, N_2)$, the results on Hopf and period-doubling bifurcations are obtained numerically. A reduced system with one herbivore and one plant species was considered in [2] and [7], in which both analytical and numerical results are provided. In [3], we used data on primary succession in the Alaska Bonanza Creek LTER to estimate model parameters and illustrated that the TDFRM very accurately simulated changes in community composition, whereas the corresponding model with Holling type II response could not be fit reasonably to the data.

In the functional response $C(N)$ given in (1), the effect of plant toxin on reducing herbivore's ingestion rate as the intake amount increases is modeled by using the factor $1 - \alpha f(N)/G$. To explore whether the new dynamics in the TDFRM are dependent on the particular functional form used to incorporate plant toxins, we consider in this paper an alternative form of the toxin-mediated functional response. In the new response, the effect of toxins is modeled as a direct increase in the handling time. We investigate how the different assumptions may affect model outcomes. As in [6], the model considered in this paper is a three-dimensional system with one herbivore population and two plant species that have different levels of toxicity. Stability and bifurcation of the system will be studied both analytically and numerically, and the results will be used to examine the role of toxin-determined functional response in plant-herbivore dynamics.

The paper is organized as the follows: in Section 2, we introduce the new toxin-determined functional response and the corresponding model, Sections 3 and 4 consider the boundary and interior equilibria, respectively, and stability and bifurcation analysis are presented with threshold conditions formulated using biologically relevant parameters. The results are discussed in Section 5.

2. **The model.** The toxin-determined functional response defined in (1) implies that the effect of plant toxins on an herbivore is a reduced growth rate when the ingested toxins exceeds the maximum tolerable amount. This is reflected by the factor $1 - f(N)/4G$ which is a part of the herbivore's growth rate. A more specific effect of the toxicant can be viewed as purely a slowdown in feeding rate. Studies have shown that toxins control herbivory by satiating the herbivory's detoxification system. When fed with plants containing toxins, the herbivore has to detoxify food in order to avoid harm from toxins, so the rate of digestion may be slower and more handling time is needed as a consequence.

Let h, e, G, and N be as defined in the previous section. Assume that in the presence of plant toxins, the toxin-adjusted handling time, denoted by $\tilde{h}$, is an increasing function of the plant amount encountered per unit of time, eN, and tends to infinity when eN approaches a maximal value determined by G. Under this assumption, the effective consumption rate becomes zero when the maximum amount of toxin allowed to ingest is reached. More specifically, the toxin-adjusted handling time $\tilde{h}(N)$ is defined by

$$\tilde{h}(N) = \begin{cases} \dfrac{h}{1 - \alpha eN/G}, & \alpha eN < G; \\ \infty, & \alpha eN \geq G, \end{cases} \tag{3}$$

where the constant α is a scaling parameter (to be chosen so that the corresponding functional response has the appropriate maximum).

The toxin-determined functional response $g(N)$ is:

$$g(N) = \frac{eN}{1 + \tilde{h}(N)eN}.$$

Replacing $\tilde{h}(N)$ by the expression in (3) we can rewrite $g(N)$ as

$$g(N) = \begin{cases} \dfrac{eN(G - \alpha eN)}{G - \alpha eN + heNG}, & \alpha eN < G; \\ 0, & \alpha eN \geq G. \end{cases} \tag{4}$$

Clearly, the function $g(N)$ is a modification of the Holling Type 2 response $f(N)$ (see (2)) with the constant handling time h replaced by the density dependent handling time $\tilde{h}(N)$. However, the two functions have very different properties. For example, $f(N)$ is an increasing function of N whereas $g(N)$ first increases to a maximum at

$$N_m = \frac{G}{e\left(\sqrt{\alpha hG} + \alpha\right)}, \tag{5}$$

and then decreases to and remains at zero (see Fig. 1). Fig. 1 shows the case of $N_m < K$, in which the maximum value of the response function is

$$g(N_m) = \frac{G}{\left(\sqrt{\alpha} + \sqrt{hG}\right)^2}.$$

In order for $g(N)$ to have G as its maximum value, i.e., $g(N_m) = G$, we need to choose α to be

$$\alpha = \left(1 - \sqrt{hG}\right)^2. \tag{6}$$

In the case when $N_m \geq K$, $g(N)$ is a monotone increasing function for N in the biologically feasible range, $0 \leq N \leq K$. A more biologically reasonable scenario is when K is much larger than N_m. Thus, in the remainder of this paper, we will focus on the case of $N_m < K$.

The functional response given in (4) can be extended to the case of two plant species. Let N_i denote the densities of plant species i $(i = 1, 2)$. Let h_i, e_i, G_i, α_i denote the corresponding parameters for species i $(i = 1, 2)$. Then the per-capita consumption rate of herbivores on plant i is

$$g_i(N_1, N_2) = \begin{cases} \dfrac{e_i N_i}{1 + \tilde{h}_1(N_1)e_1N_1 + \tilde{h}_2(N_2)e_2N_2}, & \text{if } \alpha_i e_i N_i < G_i, \quad i = 1, 2; \\ 0, & \text{otherwise,} \end{cases} \tag{7}$$

where $\tilde{h}_1(N_1)$ and $\tilde{h}_2(N_2)$ have the similar form as $h(N)$ in (3) and are given by

$$\tilde{h}_i(N_i) = \begin{cases} \dfrac{h_i}{1 - \alpha_i e_i N_i / G_i}, & \text{if } \alpha_i e_i N_i < G_i; \\ 0, & \text{if } \alpha_i e_i N_i \geq G_i, \quad i = 1, 2, \end{cases}$$

and α_i has the similar form as α in (6)

$$\alpha_i = \left(1 - \sqrt{h_i G_i}\right)^2. \tag{8}$$

Let $\mathbf{N} = (N_1, N_2)$ denote the vector of the plant densities. The model with the functional response given in (7) reads

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \Big(1 - \frac{N_1 + \beta_{12} N_2}{K_1}\Big) - P g_1(\mathbf{N}) \\ \frac{dN_2}{dt} &= r_2 N_2 \Big(1 - \frac{N_2 + \beta_{21} N_1}{K_2}\Big) - P g_2(\mathbf{N}) \\ \frac{dP}{dt} &= P\Big(B_1 g_1(\mathbf{N}) + B_2 g_2(\mathbf{N}) - D\Big). \end{aligned} \tag{9}$$

$P = P(t)$ denotes the density of herbivore at time t; r_i and K_i denote the intrinsic per capita growth rate and the carrying capacity of plant species i, respectively; β_{ij} represents the competition intensity of plant species j on plant species i; B_i is the conversion coefficient of consumed plant species i to the biomass of the herbivore; and D denotes the per capita death rate of herbivores. it is clear that if the initial plant density $N_i(0) < K_i$, then $N_i(t) < K_i$ for all $0 < t < \infty$ and $i = 1, 2$. Thus, we will restrict our attention to the region in which $N_i \leq K_i$ for $i = 1, 2$.

We remark that the system (9) has the same structure as the model studied in [6], with the only difference being that the response function $C_i(\mathbf{N})$ is replaced by $g_i(\mathbf{N})$ $(i = 1, 2)$. Gleeson and Wilson studied a system of one consumer and two resources with the standard Holling type II functional response and the Lotka-Volterra competition (see [4]). They show that an interior equilibrium (coexistence both plants and herbivore) exists, and it can be either stable or unstable. Similar to the case of one plant and one herbivore, when the interior equilibrium is unstable, a stable periodic solution may exist. More results on other consumer-resource models involving one herbivore and two plant species are discussed in [14]. However, none of these models consider explicitly the effect of toxin. It has been shown for the case of one herbivore and one plant species that systems with the Holling type II response and the toxin-determined functional response (1) can have very different dynamics (see [2, 7]).

3. **Boundary equilibria.**

In this section, we derive conditions for the existence and stability of boundary equilibria of the system (9).

3.1. **Existence of boundary equilibria.**

The system (9) has eight possible boundary equilibria. The first type of boundary equilibria are those at which herbivore is absent, i.e., $P = 0$, with either one or two plant species being present. There are four boundary equilibria of this type:

$$E_0 = (0,0,0), \quad E_1 = (K_1,0,0), \quad E_2 = (0,K_2,0), \quad \bar{E} = (\bar{N}_1, \bar{N}_2, 0), \tag{10}$$

where

$$\bar{N}_1 = \frac{K_1 - \beta_{12}K_2}{1-\beta_{12}\beta_{21}}, \quad \bar{N}_2 = \frac{K_2 - \beta_{21}K_1}{1-\beta_{12}\beta_{21}}.$$

The properties of these equilibria (existence and stability) are very similar to those of the Lotka-Volterra system, except that some of conditions may depend on parameters related to the herbivore.

E_0, E_1, and E_2 always exist. $\bar{E}$ exists if and only if

$$\frac{\beta_{21}K_1}{K_2} < 1 \quad \text{and} \quad \frac{\beta_{12}K_2}{K_1} < 1, \tag{11}$$

or

$$\frac{\beta_{21}K_1}{K_2} > 1 \quad \text{and} \quad \frac{\beta_{12}K_2}{K_1} > 1. \tag{12}$$

The second type of boundary equilibria are those at which $P > 0$, with only one plant species being present. Note that in the model the herbivore cannot survive if there is no plant. There are also four equilibria of this type:

$$\tilde{E}^{\pm} = (\tilde{N}_1^{\pm}, 0, \tilde{P}^{\pm}), \quad \hat{E}^{\pm} = (0, \hat{N_2}^{\pm}, \hat{P}^{\pm}), \tag{13}$$

with

$$\begin{aligned}
\tilde{N}_1^{\pm} &= \frac{B_1e_1 + D(a_1 - h_1e_1) \pm \sqrt{[B_1e_1 + D(a_1-h_1e_1)]^2 - 4B_1e_1a_1D}}{2B_1e_1a_1}, \\
\tilde{P}^{\pm} &= r_1\tilde{N}_1\left(1 - \frac{\tilde{N}_1^{\pm}}{K_1}\right)\frac{B_1}{D}, \\
\hat{N_2}^{\pm} &= \frac{B_2e_2 + D(a_2 - h_2e_2) \pm \sqrt{[B_2e_2 + D(a_2-h_2e_2)]^2 - 4B_2e_2a_2D}}{2B_2e_2a_2}, \\
\hat{P}^{\pm} &= r_2\hat{N}_2\left(1 - \frac{\hat{N_2}^{\pm}}{K_2}\right)\frac{B_2}{D},
\end{aligned} \tag{14}$$

where

$$a_i = \alpha_i e_i / G_i. \tag{15}$$

The existence conditions of these equilibria can be formulated using the biologically meaningful quantities

$$w_i = B_iG_i - D, \quad i = 1,2, \tag{16}$$

and

$$\begin{aligned}
w_{K1} = B_1g_1(K_1, 0) - D, &\qquad w_{K2} = B_2g_2(0, K_2) - D, \\
\bar{w} = B_1g_1(\bar{N}_1, \bar{N}_2) &+ B_2g_2(\bar{N}_1,\bar{N}_2) - D.
\end{aligned} \tag{17}$$

Notice that B_iG_i represents the maximum energy gain (or the density of new herbivore) per unit of time when only plant species i is present, and D is the energy loss per unit of time of the herbivore. Thus, $w_i = B_iG_i - D$ represents the *maximum* fitness of herbivore when only plant species i is present ($i = 1, 2$). Similarly, $B_1g_1(K_1, 0)$ is herbivore's energy gain per unit of time when plant species 1 is at its maximum density K_1 while plant 2 is absent; and thus, w_{K1} represents the herbivore's fitness when $(N_1, N_2) = (K_1, 0)$. Moreover, w_{K2} is the herbivore's fitness when $(N_1, N_2) = (0, K_2)$, and $\bar{w}$ represents the herbivore's fitness when $(N_1, N_2) = (\bar{N}_1, \bar{N}_2)$.

Note that the functions $g_1(N_1, 0)$ and $g_2(0, N_2)$ achieve their respective maximum values at $N_i = N_{im}$ with

$$N_{im} = \frac{1}{a_i + \sqrt{h_ie_ia_i}}, \quad i = 1, 2, \tag{18}$$

and

$$g_{1max} = g_1(N_{1m}, 0) = G_1, \quad g_{2max} = g_2(0, N_{2m}) = G_2. \tag{19}$$

Since $g_1(K_1, 0) < G_1$ and $g_2(0, K_2) < G_2$, we have

$$w_{Ki} < w_i. \tag{20}$$

The existence results below suggest that for the herbivore to be able to survive on only plant species i, its maximum fitness w_i must be positive.

Theorem 3.1. *Let w_i and w_{Ki} be as defined in (16) and (17).*

- *(i) $\tilde{E}$ does not exist if $w_1 < 0$ (i.e., the herbivore's maximum fitness when only species 1 is present is negative). $\hat{E}$ does not exist if $w_2 < 0$ (i.e., the herbivore's maximum fitness when only species 2 is present is negative).*
- *(ii) Both $\tilde{E}^+$ and $\tilde{E}^-$ exist when $w_{K1} < 0 \le w_1$, with $\tilde{E}^+ = \tilde{E}^-$ if $w_1 = 0$. If $w_{K1} > 0$, then $\tilde{E}^-$ exists but $\tilde{E}^+$ does not.*
- *(iii) Both $\hat{E}^+$ and $\hat{E}^-$ exist when $w_{K2} < 0 \le w_2$, with $\hat{E}^+ = \hat{E}^-$ if $w_2 = 0$. If $w_{K2} > 0$, then $\hat{E}^-$ exists but $\hat{E}^+$ does not.*

Proof. We provide the proof only for the existence of $\tilde{E}$. The proof for $\hat{E}$ follows the same argument. The components of $\tilde{E} = (\tilde{N}_1, 0, \tilde{P})$ can be calculated by solving the equations:

$$\begin{aligned} &B_1g_1(N_1, 0) = D, \\ &r_1N_1\left(1 - \frac{N_1}{K_1}\right) = Pg_1(N_1, 0). \end{aligned} \tag{21}$$

The first equation in (21) suggests that $\tilde{N}_1$ can be determined graphically by the intersection point(s) of the two curves $y = B_1g_1(N_1, 0)$ and $y = D$ (see Fig. 2). $\tilde{P}$ can be obtained easily from the second equation in (21) for a given $\tilde{N}_1 > 0$.

For Part (i), it is clear from Fig. 2 that, there is no intersection if $D > B_1G_1$, which is equivalent to $w_1 < 0$ (see Fig. 2 (a)). Thus, $\tilde{E}$ does not exist in this case.

For Part (ii), notice that if G_1 and B_1 are fixed, as D decreases (so w_1 increases), the line $y = D$ intersects the curve $y = B_1g_1(N_1, 0)$ at one point ($\tilde{N}_1^- = \tilde{N}_1^+$) when $D = B_1G_1$ (or $w_1 = 0$, see Fig. 2 (b)), and two points ($\tilde{N}_1^- < \tilde{N}_1^+$) when $B_1g_1(K_1, 0) < D < B_1G_1$ (or $w_{K1} < 0 < w_1$, see Fig. 2 (c)). Thus, there is a unique $\tilde{E}$ when $w_1 = 0$ and two equilibria $\tilde{E}^\pm$ when $w_{K1} < 0 < w_1$. As D continues to decrease such that $D < B_1g_1(K_1, 0)$ (or $w_{K1} > 0$), $\tilde{N}_1^+$ increases and exceeds K_1 (see Fig. 2 (d)). Thus, $\tilde{E}^-$ exists but $\tilde{E}^+$ does not.

Similar arguments can be used to prove Part (iii) for the existence of $\hat{E}^{\pm}$, which is omitted here. This completes the proof of the theorem. $\square$

3.2. **Stability of boundary equilibria.** We first consider the stability of the four equilibria listed in (10). Results for these equilibria are summarized in the following theorem.

Theorem 3.2. *Let w_{Ki} be as defined in (17). Then*

(a) E_0 is always unstable;

(b) E_1 is locally asymptotically stable (l.a.s.) if $\dfrac{\beta_{21}K_1}{K_2} > 1$ and $w_{K1} < 0$;

(c) E_2 is l.a.s. if $\dfrac{\beta_{12}K_2}{K_1} > 1$ and $w_{K2} < 0$;

(d) $\bar{E}$ is l.a.s. if the conditions in (11) hold and $\bar{w} < 0$.

This theorem can be easily proved by looking at the eigenvalues of the corresponding Jacobian matrices. We remark that the stability conditions are very similar to those of Lotka-Volterra system for two competing species (in the absence of herbivore). The additional condition, $w_{Ki} < 0$, implies that the herbivore will go extinct due to the negative fitness. The condition $\beta_{ij}K_j/K_i > 1 (< 1)$ implies a strong (weak) competition pressure from plant species j on i. Thus, the results suggest that in the absence of herbivore, a plant species will go extinct if there is a strong competition from the other species. As will be shown in the next section, these results may change in the presence of herbivore and when the influence of plant toxicity is sufficiently high.

To formulate the stability conditions for the second set of boundary equilibria listed in (13), besides w_i and w_{Ki}, we will also use the plant growth rate r_i to describe the threshold conditions for stability. For ease of presentation, we assume throughout this section that the following conditions hold

$$G_i < \frac{1}{h_i}, \quad N_{im} < K_i, \quad \alpha_i e_i K_i < G_i, \quad i = 1, 2. \tag{22}$$

Recall that the first condition implies that the maximum intake rate G_i of plant i is lower than $1/h_i$ which is the maximum intake rate in the absence of toxins ($i = 1, 2$). The second condition implies that the plant density N_{im} at which the herbivore achieves the maximum intake rate (G_i) is to the left of K_i, so that the curves $g_1(N_1, 0)$ and $g_2(0, N_2)$ are not monotone on the intervals $(0, K_1)$ and $(0, K_2)$ respectively (see Section 5 for a discussion about the case $N_{im} > K_i$). The third condition implies the toxin-adjusted handling time $\tilde{h}_i(N_i)$ is finite for all plant density $N_i < K_i$, which in turn implies that $g_1(N_1, 0) > 0$ and $g_2(0, N_2) > 0$ for all $N_i < K_i$, $i = 1, 2$ (see (7)). The stability results of the equilibria $\tilde{E}^{\pm}$ are given below.

Theorem 3.3. *Let*

$$w_1 > 0, \quad \frac{\beta_{21}K_1}{K_2} < 1, \quad \text{and} \quad G_1 < \frac{1}{4h_1}. \tag{23}$$

(a) The equilibrium $\tilde{E}^{+}$ is always unstable;

(b) There exist constants $\sigma_{1c} > 0$ and $w_{1c} > 0$, such that $\tilde{E}^{-}$ is l.a.s. if $\dfrac{r_1}{r_2} > \sigma_{1c}$ and $w_1 > w_{1c}$, and unstable if either $\dfrac{r_1}{r_2} < \sigma_{1c}$ or $w_1 < w_{1c}$;

(c) When $\dfrac{r_1}{r_2} > \sigma_{1c}$*, a Hopf bifurcation occurs at* $w_1 = w_{1c}$*, and stabile periodic solutions exist for* w_1 *near* w_{1c} *and* $w_1 < w_{1c}$*.*

Proof. The Jacobian matrix at the equilibrium point $\tilde{E}^{\pm}$ is

$$\tilde{J}^{\pm} = \begin{pmatrix} 0 & b_1^{\pm} & * \\ b_2^{\pm} & b_3^{\pm} & * \\ 0 & 0 & b_4^{\pm} \end{pmatrix},$$

where

$$\begin{aligned} b_1^{\pm} &= \tilde{P}^{\pm} B_1 \frac{\partial g_1}{\partial N_1}(\tilde{N}_1^{\pm}, 0), \\ b_2^{\pm} &= -g_1(\tilde{N}_1^{\pm}, 0), \\ b_3^{\pm} &= r_1\left(1 - \frac{2\tilde{N}_1^{\pm}}{K_1}\right) - \tilde{P}^{\pm}\frac{\partial g_1}{\partial N_1}(\tilde{N}_1^{\pm}, 0), \\ b_4^{\pm} &= r_2\left(1 - \frac{\beta_{21}\tilde{N}_1^{\pm}}{K_2}\right) - \tilde{P}^{\pm}\frac{\partial g_2}{\partial N_2}(\tilde{N}_1^{\pm}, 0), \end{aligned}$$

and the other two entries have no effect on the stability of the equilibrium, which are denoted by an "$*$".

The matrix $\tilde{J}^{\pm}$ has one eigenvalue $b_4^{\pm}$ and two other eigenvalues are the same as that of the matrix

$$\tilde{M}^{\pm} = \begin{pmatrix} 0 & b_1^{\pm} \\ b_2^{\pm} & b_3^{\pm} \end{pmatrix}.$$

Thus, $\tilde{E}^{\pm}$ is l.a.s. if

$$b_1^{\pm} b_2^{\pm} < 0, \quad b_3^{\pm} < 0, \quad \text{and} \quad b_4^{\pm} < 0. \tag{24}$$

Notice that $\tilde{P}^{+} > 0$, $g_1(\tilde{N}_1^{+}, 0) > 0$, and $\dfrac{\partial g_1}{\partial N_1}(\tilde{N}_1^{+}, 0) < 0$, we have

$$b_1^{+} b_2^{+} = -\tilde{P}^{+} B_1 g_1(\tilde{N}_1^{+}, 0)\frac{\partial g_1}{\partial N_1}(\tilde{N}_1^{+}, 0) > 0.$$

This shows that $\tilde{E}^{+}$ is always unstable, and part (a) is proved.

Next, we consider the stability of $\tilde{E}^{-}$. The Jacobian matrix $\tilde{J}^{-}$ has one eigenvalue b_4^{-}, which may correspond to one set of condition, and two other eigenvalues determined by the matrix $\tilde{M}^{-}$, which will correspond to another set of conditions. Substitution of

$$\tilde{P}^{-} = r_1 \tilde{N}_1^{-}\left(1 - \frac{\tilde{N}_1^{-}}{K_1}\right)\frac{1}{g_1(\tilde{N}_1^{-}, 0)} \tag{25}$$

in b_4^{-} yields

$$b_4^{-} = r_2\left(1 - \frac{\beta_{21}\tilde{N}_1^{-}}{K_2}\right) - \frac{r_1 e_2}{e_1}\left(1 - \frac{\tilde{N}_1^{-}}{K_1}\right). \tag{26}$$

Let

$$\sigma_{1c} = \frac{e_1\left(1 - \dfrac{\beta_{21}\tilde{N}_1^-}{K_2}\right)}{e_2\left(1 - \dfrac{\tilde{N}_1^-}{K_1}\right)}, \tag{27}$$

where $\tilde{N}_1^-$ is given in (14) and is independent of r_1 and r_2. Then from (26) and (27),

$$b_4^- < 0 \quad \Longleftrightarrow \quad \frac{r_1}{r_2} > \sigma_{1c}. \tag{28}$$

Since $\beta_{21}\tilde{N}_1^-/K_2 < \beta_{21}K_1/K_2 < 1$ (assumption) and $\tilde{N}_1^- < K_1$, we know that $\sigma_{1c} > 0$.

For the product $b_1^- b_2^-$, because $\tilde{P}^- > 0$, $g_1(\tilde{N}_1^-, 0) > 0$, and $\dfrac{\partial g_1}{\partial N_1}(\tilde{N}_1^-, 0) > 0$, then we have

$$b_1^- b_2^- = -\tilde{P}^- B_1 g_1(\tilde{N}_1^-, 0)\frac{\partial g_1}{\partial N_1}(\tilde{N}_1^-, 0) < 0. \tag{29}$$

We now examine the sign of b_3^-. Substituting the expression in (25) for $\tilde{P}^-$ in b_3^- we get

$$b_3^- = b_3^-(\tilde{N}_1^-) = \psi(\tilde{N}_1^-)F(\tilde{N}_1^-), \tag{30}$$

where $\tilde{N}_1^-$ is given in (14), and the functions ψ and F are given by

$$\begin{aligned} \psi(N_1) &= \frac{r_1 N_1}{(1 - a_1N_1)^2 + h_1e_1N_1(1 - a_1N_1)}\,\frac{a_1 - h_1e_1}{K_1}, \\ F(N_1) &= -a_1N_1^2 + 2N_1 + \frac{h_1e_1K_1 - 1}{a_1 - h_1e_1}. \end{aligned} \tag{31}$$

From (8), (15), and the assumption $G_1 < 1/(4h_1)$ we have

$$a_1 - h_1e_1 = \frac{e_1}{G_1}(\alpha_1 - h_1G_1) = \frac{e_1}{G_1}\left(1 - 2\sqrt{h_1G_1}\right) > 0, \tag{32}$$

and from (15) and (22) we know that for $N_1 \le N_{1m} < K_1$,

$$1 - a_1N_1 > 1 - a_1K_1 = \frac{1}{G_1}\left(G_1 - \alpha_1e_1K_1\right) > 0. \tag{33}$$

The inequalities (32) and (33) imply that $\psi(N_1) > 0$ for $N_1 < N_{1m}$. Thus, from (30) we know that the two functions $b_3^-(\tilde{N}_1^-)$ and $F(\tilde{N}_1^-)$ have the same sign and same zeros.

We now examine the possibility that $F(N_1)$ has a zero for some $N_1 = \tilde{N}_1^-$. Since $a_1 - h_1e_1 > 0$ and $h_1e_1K_1 - 1 < a_1K_1 - 1 < 0$ (see (32) and (33)), we have

$$F(0) = \frac{h_1e_1K_1 - 1}{a_1 - h_1e_1} < 0.$$

As $a_1 > 0$, the curve of $F(N_1)$ is a parabola with its maximum at $N_{1F} = 1/a_1$. Note that $\alpha_1e_1N_{1m} < G_1$, i.e., $N_{1m} < G_1/\alpha_1e_1 = 1/a_1$. Thus, $N_{1m} < N_{1F}$, which implies that $F(N_1)$ increases monotonically for $N_1 \in (0, N_{1m})$ (see Fig. 3). Using the expression in (18) for N_{1m} we get

$$F(N_{1m}) = \frac{h_1e_1K_1}{a_1 - h_1e_1}\left(1 - \frac{2N_{1m}}{K_1}\right).$$

From $h_1e_1 < a_1$ and $a_1K_1 < 1$ (see (32) and (33)), we have

$$2N_{1m} = \frac{2}{a_1 + \sqrt{h_1 e_1 a_1}} > \frac{1}{a_1} > K_1.$$

It follows that $F(N_{1m}) > 0$. Therefore, there exists a unique $N_1^* \in (0, N_{1m})$ such that

$$F(N_1^*) = 0, \qquad \text{and} \qquad \frac{\partial F}{\partial N_1} > 0 \quad \text{for } N_1^* \in (0, N_{1m}) \tag{34}$$

(see Fig. 3). In fact, N_1^* can be solved explicitly:

$$N_1{}^* = \frac{1}{a_1} - \frac{1}{a_1}\sqrt{\frac{h_1 e_1 (1 - a_1 K_1)}{(a_1 - h_1 e_1)}}. \tag{35}$$

It remains to show that N_1^* is a solution of the equation

$$B_1 g_1(N_1, 0) = D \tag{36}$$

(so that it is the component of $\tilde{E}^-$) corresponding to a critical value w_{1c}. Recall that $w_1 = B_1 G_1 - D$ is the herbivore's maximum fitness and has been chosen to be the bifurcation parameter (assuming that B_1 and G_1 are fixed so that w_1 varies as D varies).

In order to use the above identified N_1^* to define a threshold value w_{1c}, we first show that $\tilde{N}_1^-$ is a monotonically decreasing function of w_1. Notice that $\tilde{N}_1^-$ is the intersection point of the curves $y = B_1 g_1(N_1, 0)$ and $y = D$ on the left of N_{1m} (see Fig. 3), and that $B_1 g_1(N_1, 0)$ is a monotone function of N_1 on $(0, N_{1m})$. It is clear from Fig. 3 that for each $D \in (0, B_1 G_1)$, a unique $\tilde{N}_1^-$ can be solved from the equation (36), which will define a monotone increasing function $\tilde{N}_1^- = \tilde{N}_1^-(D)$. The monotonicity also implies that there exist a $D^* \in (0, B_1 G_1)$ such that $\tilde{N}_1^-(D^*) = N^*$. Since $D = D(w_1) = B_1 G_1 - w_1$ is a strictly decreasing function of w_1 on $(0, B_1 G_1)$, we know that

$$\tilde{N}_1^-(w_1) = \tilde{N}_1^-(D(w_1)) \tag{37}$$

defines a monotone decreasing function of w_1 on $(0, B_1 G_1)$ with range $(0, N_{1m})$. As $N_1^* \in (0, N_{1m})$, from the Intermediate Value Theorem, there exists a $w_{1c} \in (0, B_1 G_1)$ such that

$$\tilde{N}_1^-(w_{1c}) = N_1^*. \tag{38}$$

Moreover,

$$\frac{\partial \tilde{N}_1^-}{\partial w_1} < 0 \qquad \text{for } \; 0 < w_1 < B_1 G_1. \tag{39}$$

Since $b_3^-(\tilde{N}_1^-(w_1))$ and $F(\tilde{N}_1^-(w_1))$ have the same sign and same zeros, from (34) and (37)–(39) we know that

$$b_3^- = \begin{cases} < 0 & \text{for } w_1 > w_{1c}, \\ = 0 & \text{for } w_1 = w_{1c}, \\ > 0 & \text{for } w_1 < w_{1c}. \end{cases} \tag{40}$$

It follows that $\tilde{E}^-$ is l.a.s. if $r_1/r_2 > \sigma_{1c}$ and $w_1 > w_{1c}$, and unstable if either $r_1/r_2 < \sigma_{1c}$ or $w_1 < w_{1c}$. It is easy to check that $w_{1c} > 0$ as

$$w_{c1} = B_1 G_1 - D^* = B_1 G_1 - B_1 g_1(N_1^*, 0) = B_1\big(G_1 - g_1(N_1^*, 0)\big)$$

and $g_1(N_1^*, 0) < G_1$. This completes the proof of part (b).

For Part (c), notice that the Jacobian matrix $\tilde{J}^-$ at $\tilde{E}^-$ has one negative eigenvalue $\tilde{b}_4^-$ and two other eigenvalues given by

$$\lambda = \frac{b_3^- \pm \sqrt{(b_3^-)^2 + 4b_1^- b_2^-}}{2}. \tag{41}$$

From (29) we have $b_1^- b_2^- < 0$. Notice from (40) that $b_3^-(w_{1c}) = 0$. Thus, as a function of w_1, $\lambda(w_1)$ is pure imaginary at $w_1 = w_{1c}$. That is,

$$\Re(\lambda(w_{1c})) = \frac{b_3^-(w_{1c})}{2} = 0, \quad \Im(\lambda(w_{1c})) = \pm\sqrt{-b_1^- b_2^-} \neq 0.$$

Since $\tilde{N}_1^-(w_{1c}) = N_1^*$ (see (38)) and $F(N_1^*) = 0$ (see (34)), using these facts and the expression for $b_3^- = b_3^-(\tilde{N}_1^-(w_1))$ (see (30)) we have

$$\begin{aligned} \frac{\partial \Re(\lambda)}{\partial w_1}\Big|_{w_1 = w_{1c}} &= \frac{1}{2}\Big(\frac{\partial b_3^-}{\partial \tilde{N}_1^-}\Big|_{\tilde{N}_1^- = N^*}\Big)\Big(\frac{\partial \tilde{N}_1^-}{\partial w_1}\Big|_{w_1 = w_{1c}}\Big) \\ &= \frac{1}{2}H(N_1^*)\Big(\frac{\partial F}{\partial \tilde{N}_1^-}\Big|_{\tilde{N}_1^- = N^*}\Big)\Big(\frac{\partial \tilde{N}_1^-}{\partial w_1}\Big|_{w_1 = w_{1c}}\Big), \end{aligned} \tag{42}$$

where

$$H(N_1^*) = \frac{a_1 - h_1 e_1}{K_1} \frac{r_1 {N_1}^*}{(1 - a_1 {N_1}^*)^2 + h_1 e_1 {N_1}^*(1 - a_1 {N_1}^*)}.$$

From (32) and (33) we have $H(N^*) > 0$. Since $F(N_1)$ increases with N_1 and $\tilde{N}_1^-$ decreases with w_1, we know that

$$\frac{\partial F}{\partial \tilde{N}_1^-}\Big|_{\tilde{N}_1^- = N^*} > 0, \quad \frac{\partial \tilde{N}_1^-}{\partial w_1}\Big|_{w_1 = w_{1c}} < 0.$$

It follows from (42) that $\frac{\partial \Re(\lambda)}{\partial w_1}\Big|_{w_1 = w_{1c}} < 0$. Thus, as w_1 decreases and passes w_{1c}, the equilibrium $\tilde{E}^-$ changes from stable to unstable, and stable periodic solutions exist for $w_1 < w_{1c}$ and near w_{1c}. Therefore, there exists a Hopf bifurcation at the point $w_1 = w_{1c}^-$, and stable periodic solutions exist for w_1 near w_{1c}^- with $w_1 < w_{1c}^-$.

This completes the proof. □

The stability of $\hat{E}^\pm$ are stated in the following Theorem, which can be proved in a similar way as for $\tilde{E}^\pm$.

Theorem 3.4. *Let* $w_2 > 0$, $\frac{\beta_{12} K_2}{K_1} < 1$, *and* $G_2 < \frac{1}{4h_2}$.

(a) The equilibrium $\hat{E}^+$ *is always unstable;*

(b) There exist constants $\sigma_{2c} > 0$ *and* $w_{2c} > 0$, *such that* $\hat{E}^-$ *is l.a.s. if* $\frac{r_2}{r_1} > \sigma_{2c}$ *and* $w_2 > w_{2c}$, *and unstable if either* $\frac{r_2}{r_1} < \sigma_{2c}$ *or* $w_2 < w_{2c}$;

(c) When $\frac{r_2}{r_1} > \sigma_{2c}$, *a supercritical Hopf bifurcation occurs at* $w_2 = w_{2c}$.

We remark that the sets of stability conditions (see, for example, (23)) identified in this section are sufficient but not necessary. There are other scenarios in which the equilibria $\tilde{E}^-$ and $\hat{E}^-$ may be stable. Nonetheless, these results provide useful insights into the role of plant toxicity in the composition of plant community. For example, the condition $\beta_{21} K_1 / K_2 < 1$ in (23) implies that plant species 1 is a weaker competitor and cannot excluded plant species 2 in the absence of herbivore (independent of their growth rates). However, Theorem 3.3 suggests that in the presence of herbivore, if plant 1 has a relatively high growth rate ($r_1/r_2 > \sigma_{1c}$) and higher toxicity (smaller G_1 value, see (23)), then it is possible for plant 1 to exclude plant 2 (as $\tilde{E}^-$ is l.a.s.).

4. Interior equilibrium.

Due to the non-linearity of $g_i(N_1, N_2)$ ($i = 1, 2$), it is not easy to analyze the existence and stability of interior equilibria under general conditions. In this section, we identify specific regions in the parameter space in which an interior equilibrium exists. Most of the conditions are motivated by biological consideration. We provide analytical results for the existence of an interior equilibrium and use numerical simulations to explore possible stability scenarios and bifurcations.

4.1. Existence of an interior equilibrium.

Let $E^* = (P^*, N_1^*, N_2^*)$ denote an interior equilibrium of the system (9), i.e., all components of E^* are positive. Then N_1^* and N_2^* satisfy the equations:

$$\begin{aligned} &B_1e_1N_1 + B_2e_2N_2 - D\left(1 + \frac{h_1e_1N_1}{1-a_1N_1} + \frac{h_2e_2N_2}{1-a_2N_2}\right) = 0, \\ &\frac{r_1}{e_1}\left(1 - \frac{N_1+\beta_{12}N_2}{K_1}\right) - \frac{r_2}{e_2}\left(1 - \frac{N_2+\beta_{21}N_1}{K_2}\right) = 0. \end{aligned} \tag{43}$$

It is clear that N_i^* is a solution of a cubic equation. Thus, it is very difficult to obtain a general existence condition. In the following result, we consider a specific set of conditions under which an interior equilibrium exists.

As coexistence is more likely when boundary equilibria are unstable, we assume that

$$w_{Ki} > 0, \quad i = 1, 2, \tag{44}$$

in this case E_1 and E_2 are both unstable (see Theorem 3.2), and that the conditions in (11) and (12) do not hold, in which case $\bar{E}$ is unstable. One of the possibilities for this is

$$\frac{\beta_{21}K_1}{K_2} < 1 \quad \text{and} \quad \frac{\beta_{12}K_2}{K_1} > 1. \tag{45}$$

The conditions in (45) also implies that plant species 1 is a weaker competitor than species 2. To balance this we choose other parameters so that plant species 1 has certain advantages over species 2. One example of this is the following:

$$\frac{r_1}{r_2} > \frac{e_1}{e_2}, \tag{46}$$

i.e., the ratio of plant growth rates of species 1 to 2 is higher than the ratio of encounter rates (by the herbivore) of species 1 to 2. We point out that the particular choices of these assumptions are for the purpose of illustration. Many other conditions can also lead to the existence of an interior equilibrium.

Let

$$N_1^\diamond = \frac{K_1\left(\dfrac{r_1}{r_2} - \dfrac{e_1}{e_2}\right)}{\dfrac{r_1}{r_2} - \dfrac{e_1}{e_2}\dfrac{\beta_{21}K_1}{K_2}}, \quad N_2^\diamond = \frac{K_2\left(\dfrac{r_1}{r_2} - \dfrac{e_1}{e_2}\right)}{\dfrac{r_1}{r_2}\dfrac{\beta_{12}K_2}{K_1} - \dfrac{e_1}{e_2}}. \tag{47}$$

From (45) and (46) we have

$$0 < N_i^\diamond < K_i, \quad i = 1, 2. \tag{48}$$

Then the existence condition for E^* can be determined by using the following quantities

$$w_1^\diamond = B_1 g_1(N_1^\diamond, 0) - D \quad \text{and} \quad w_2^\diamond = B_2 g_2(0, N_2^\diamond) - D, \tag{49}$$

which represent the herbivore's fitness when the plant densities (only one plant species is present) are $N_1^\diamond$ and $N_2^\diamond$, respectively.

Theorem 4.1. *Suppose that conditions (44), (45), and (46) hold. System (9) has an interior equilibrium* $E^* = (P^*, N_1^*, N_2^*)$ *if*

$$w_1^\diamond w_2^\diamond < 0. \tag{50}$$

Proof. Note that all components of E^* are positive and satisfy the following equations:

$$\begin{aligned} &B_1 g_1(N_1, N_2) + B_2 g_2(N_1, N_2) - D = 0, \\ &r_1\left(1 - \frac{N_1 + \beta_{12} N_2}{K_1}\right) - P\frac{g_1(N_1, N_2)}{N_1} = 0, \\ &r_2\left(1 - \frac{N_2 + \beta_{21} N_1}{K_2}\right) - P\frac{g_2(N_1, N_2)}{N_2} = 0. \end{aligned} \tag{51}$$

Using the last two equations in (51) we get

$$\frac{r_1\left(1 - \dfrac{N_1 + \beta_{12} N_2}{K_1}\right)}{r_2\left(1 - \dfrac{N_2 + \beta_{21} N_1}{K_2}\right)} = \frac{e_1}{e_2},$$

from which we can solve for N_2 as a function of N_1:

$$N_2 = N_2^\diamond\left(1 - \frac{N_1}{N_1^\diamond}\right) := \phi(N_1), \tag{52}$$

where $N_1^\diamond$ and $N_2^\diamond$ are given in (47). Substituting $\phi(N_1)$ for N_2 in the first equation in (51) we arrive at the following equation for N_1:

$$Q(N_1) := B_1 g_1\big(N_1, \phi(N_1)\big) + B_2 g_2\big(N_1, \phi(N_1)\big) - D = 0. \tag{53}$$

From (52) we have $\phi(0) = N_2^\diamond$, $\phi(N_1^\diamond) = 0$, and from (49),

$$g_1(0, \phi(0)) = 0, \quad g_1(N_1^\diamond, \phi(N_1^\diamond)) = w_1^\diamond,$$

$$g_2(0, \phi(0)) = w_2^\diamond, \quad g_2(N_1^\diamond, \phi(N_1^\diamond)) = 0.$$

Thus,

$$Q(0) = w_2^\diamond \quad \text{and} \quad Q(N_1^\diamond) = w_1^\diamond.$$

The condition in (50) implies that $Q(0)$ and $Q(N_1^\diamond)$ have opposite signs. Thus, there exists an N_1^* with $0 < N_1^* < N_1^\diamond < K_1$, such that $Q(N_1^*) = 0$. This gives the N_1 component of E^*.

The N_2 component of E^* is obtained from (52), i.e., $N_2^* = \phi(N_1^*) < N_2^\diamond$. Since $0 < N_2^\diamond < K_2$ (see (48)), $0 < N_2^* < K_2$.

For the P component of E^*, we can use the second equation in (51) to get

$$P^* = r_1\left(1 - \frac{N_1^* + \beta_{12}N_2^*}{K_1}\right)\frac{N_1^*}{g_1(N_1^*, N_2^*)}.$$

It remains to show that P^* is positive. Clearly, $g_1(N_1^*, N_2^*) > 0$ as $0 < N_i^* < K_i$ $(i = 1, 2)$. Thus, we only need to show that

$$1 - \frac{N_1^* + \beta_{12}N_2^*}{K_1} > 0.$$

Replacing N_2^* by $\phi(N_1^*)$ we have

$$1 - \frac{N_1^* + \beta_{12}N_2^*}{K_1} = \frac{e_1/e_2}{\dfrac{K_1}{K_2}\left(\dfrac{r_1}{r_2}\dfrac{\beta_{12}K_2}{K_1} - \dfrac{e_1}{e_2}\right)}\left[\beta_{12} - \frac{K_1}{K_2} + \frac{N_1^*}{K_2}(1 - \beta_{12}\beta_{21})\right]. \tag{54}$$

From (45) and (46) we know that the first factor in (54) is positive as

$$\frac{r_1}{r_2}\frac{\beta_{12}K_2}{K_1} - \frac{e_1}{e_2} > \frac{r_1}{r_2} - \frac{e_1}{e_2} > 0.$$

For the second factor in (54), if $\beta_{12}\beta_{21} \le 1$ then it is clearly positive as $\beta_{12} - \dfrac{K_1}{K_2} > 0$ (from (46)). If $\beta_{12}\beta_{21} > 1$, then from $N_1^* < K_1$ and $\beta_{21}K_1/K_2 < 1$ (see (46)) we have

$$\beta_{12} - \frac{K_1}{K_2} + \frac{N_1^*}{K_2}(1 - \beta_{12}\beta_{21}) > \beta_{12} - \frac{K_1}{K_2} + \frac{K_1}{K_2}(1 - \beta_{12}\beta_{21}) = \beta_{12}\left(1 - \frac{\beta_{21}K_1}{K_2}\right) > 0.$$

Thus, the second factor in (54) is also positive. It follows that $P^* > 0$. Therefore, E^* is an interior equilibrium of the system (9). □

4.2. **Stability of E^* and bifurcations.** Results in this section are obtained from numerical simulations of the system (9). The analytic results obtained in Section 4.1 for the existence of E^* may provide a guidance for the selection of parameter values used in the numerical studies in this section. In addition, for comparison purposes, parameters are also chosen in the similar regions as those in [6].

As was done in [6], we used the computer program AUTO to generate a bifurcation diagram near the interior equilibrium E^*. Recall that most of our analytic results in the previous sections are formulated based on a quantity that measures the herbivore's fitness when plant densities are N_1 and N_2:

$$w_{Ni} = B_i g_i(N_1, N_2) - D, \quad i = 1, 2$$

(e.g., $w_i = B_iG_i - D$, $i = 1, 2$, $w_{K1} = B_1g_1(K_1, 0) - D$, $w_{K2} = B_2g_2(K_2, 0) - D$, etc.). It is possible to use these quantities to conduct numerical simulations. However, as one of the main purposes of this paper is to compare the new functional response $g_i(N_1, N_2)$ with the previous functional response $C_i(N_1, N_2)$ used in [6] in terms of their influence in the model behaviors, we use β_{12} as the bifurcation parameter in the simulations (as was done in [6]). The reason to very β_{12} was to look at how the coefficient of competitive effect of plant species 2 on 1 may affect the plant-herbivore dynamics.

Fig. 4 shows a bifurcation diagram calculated using AUTO. We observe that, for smaller values of β_{12} there is a stable interior equilibrium (thick solid curves). As β_{12} increases, a bifurcation (HB) occurs at some critical point, after which the interior equilibrium becomes unstable and a stable periodic solutions exists (the maximum values of these solutions are indicated by ▲ , ●, ♦). As β_{12} continues to increase, period-doubling (PD) solutions appears (maximum of these solutions are indicated by △, ○, ◊). Similar bifurcations also occur as β_{12} decreases from the right end. This is very similar to the case when the functional response $C(N_1, N_2)$ is used (see Fig. 5 in [6]). The labels for values of β_{12} on the x-axis are $\beta_{12} \times 10^5$. Other parameter values used are similar to those used in [6]: r_1=0.00167, r_2=0.0028, K_1=50000, K_2=150000, β_{21}=2.5, e_1=0.0001, e_2=0.0005, h_1=1/16, h_2=1/200, G_1=8, G_2=100,B_1=0.00001, B_2=0.000056, D=0.000114.

Fig. 5 presents time plots for various values of β_{12}. In Fig. 4 (a), $\beta_{12} \times 10^5 = 0.3$ is chosen from the interval in which E^* is l.a.s. and the figure shows that the solution converges to an interior equilibrium. In Fig. 4 (b), $\beta_{12} \times 10^5 = 1.5$ belongs to the region in which a stable periodic solution exists, and the figure illustrates a stable period solution. In Fig. 4 (c), $\beta_{12} \times 10^5 = 5$ is in the region in which a stable period-doubling solution exists, which is shown in the figure. In Fig. 4 (d), $\beta_{12} \times 10^5 = 8$, at which a stable interior equilibrium exists. All parameter values are the same as in Fig. 4.

5. **Discussion.**

In this paper, we considered an alternative toxin-determined functional response, $g(N)$ (see (4)), which is based on the traditional Holling Type 2 functional response (see $f(N)$ given in (2)) with a modified handling time due to plant toxins (see $\tilde{h}(N)$ given in (3)). The new toxin-determined functional response $g(N)$ is not a monotone function of plant density N. This makes it possible for the plant-herbivore system to have multiple interior equilibria, and exhibit more complex dynamics than that of models with Holling Type 2 response. We have previously studied in [6] another toxin-determined functional response (see $C(N)$ in (1)), which uses a different functional form to incorporate the reduction in herbivore's intake due to toxins. Our results suggest that models with the two toxin-determined functional responses, $C(N)$ and $g(N)$, have similar qualitative behaviors as discussed below.

The model studied in this paper is a 3-dimensional system including one herbivore population and two plant species (see (9)). Our analysis has focused on the case when $g_1(N_1, 0)$ and $g_2(0, N_2)$ first increase to their maximum values (G_1 and G_2) at N_{1m} and N_{2m}, respectively, with $N_{im} < K_i$ $(i = 1, 2)$, and then decrease for $N_i > N_{im}$. Thus, both functions are not monotone. Consequently, the system has up to eight boundary equilibria and possible multiple interior equilibria. We derived threshold conditions for the existence and stability of all boundary equilibria, with the conditions expressed using biological relevant quantities (e.g., herbivore's fitness w_i, w_{Ki}, $i = 1, 2$, etc.). We also identified a set of sufficient conditions for an interior (coexistence) equilibrium to exist. Numerical studies indicate that the system has a stable interior equilibrium for parameter values in a certain range, and that the stability switches at some critical points at which Hopf bifurcations occur. Period-doubling bifurcations may also be possible.

The model considered in [6] has the same structure as (9) except that it uses a different functional response ($C(N)$). Numerical simulations in [6] also identified Hopf bifurcations (from an interior equilibrium) and period-doubling bifurcations when the same bifurcation parameter is used. In this sense, the two toxin-determined functional responses generate similar bifurcation behaviors in the models for plant-herbivore interactions. We have also conducted numerical simulations for the system (9) in the case when $g_1(N_1, 0)$ and $g_2(0, N_2)$ are both monotone (i.e., when

$N_{im} > K_i$, $i = 1, 2$). Some of the outcomes are illustrated in Fig. 6 and 7. We observe from Fig. 6 that, while the Hopf bifurcations are still present, there is no period-doubling bifurcation.

We need to point out that the functional response $C(N)$ can also be unimodal when the plant toxicity is high (i.e., when the value of G is small), in which case $C(N)$ increases to its maximum value G at some plant density $N_m < K$, and then becomes decreasing for $N > N_m$. In this case, the 3-D system is very difficult to analyze. We have also studied a reduced 2-D system with one-herbivore and one-plant species, in which case more analytical results are possible to obtain including the threshold conditions for Hopf and homoclinic bifurcations (see [2] and [7]). It is possible to extend the stable periodic solution in the 2-D system to the 3-D system by applying some tools in dynamical systems theory. These results will be published elsewhere.

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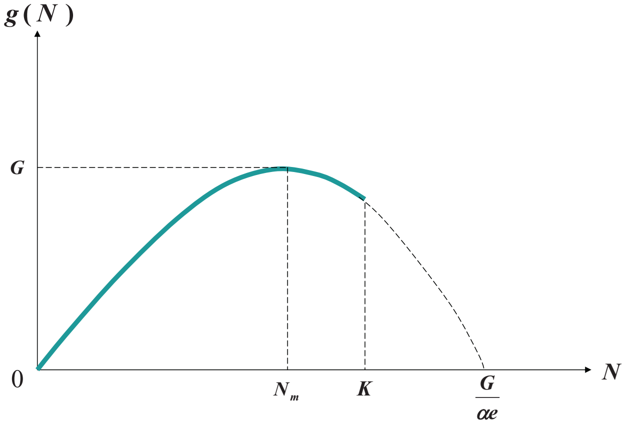

FIGURE 1. The toxin-determined functional response $g(N)$.

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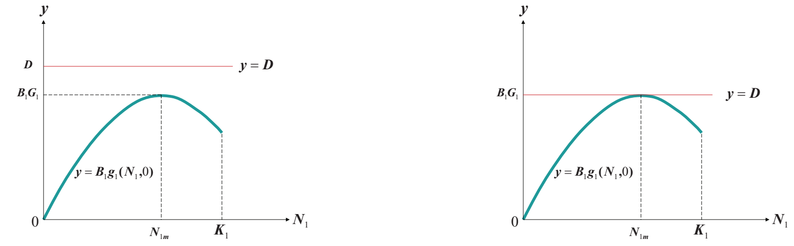
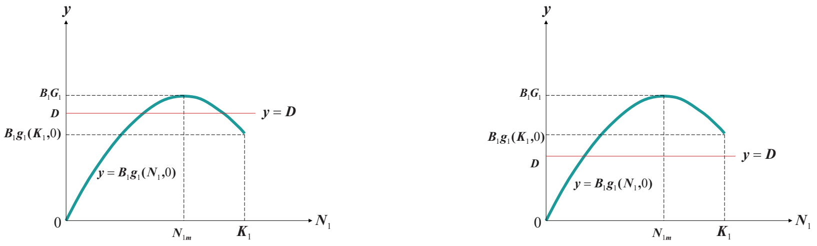


(a) $B_1G_1 < D$ (or $w_1 < 0$) (b) $B_1G_1 = D$ (or $w_1 = 0$)



(c) $B_1g_1(K_1, 0) < D < B_1G_1$ (or $w_{K1} < 0 < w_1$) (d) $B_1g_1(K_1, 0) > D$(or $w_{K1} > 0$)

FIGURE 2. Plots of $y = B_1g_1(N_1, 0)$ and $y = D$. Each intersection of the two curves (with $N_1 < K_1$) corresponds to an equilibrium $\tilde{E}$. When there are two intersections, the lower and higher values of N_1 value correspond to $\tilde{E}^-$ and $\tilde{E}^+$ respectively.

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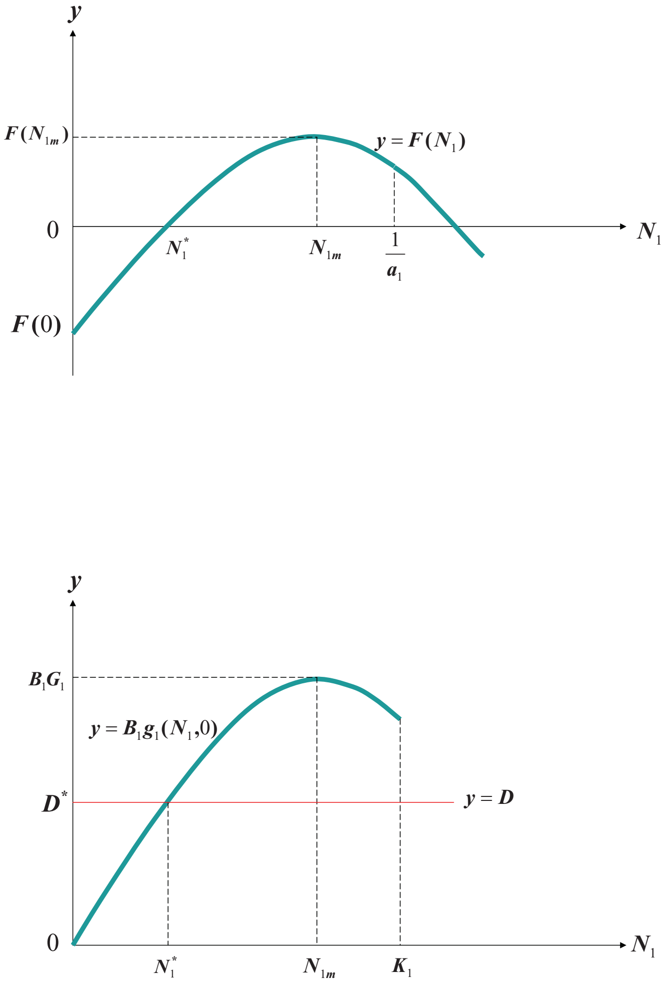

FIGURE 3. Plots of $F(N_1)$ (top, see (31) for the definition of $F(N_1)$) and $B_1g_1(N_1,0)$ (bottom). The top figure shows that $F(0) < 0$, $F(N_{1m}) > 0$, and $N_{1m} < \dfrac{1}{a_1}$, which suggests that $F(N_1)$ is a monotone increasing function for $N_1 \in (0, N_{1m})$ and that there exists a unique $N_1^* \in (0, N_{1m})$ such that $F(N_1^*) = 0$. In the bottom figure, the (smaller) intersection point of the curves $y = B_1g_1(N_1,0)$ and $y = D$ gives the value of $\tilde{N}_1^-$ (the N_1 component of the equilibrium $\tilde{E}^-$). Particularly, for the value N_1^* with $F(N_1^*) = 0$, there exists a unique $D^* \in (0, B_1G_1)$ such that $\tilde{N}_1^-(D^*) = N_1^*$.

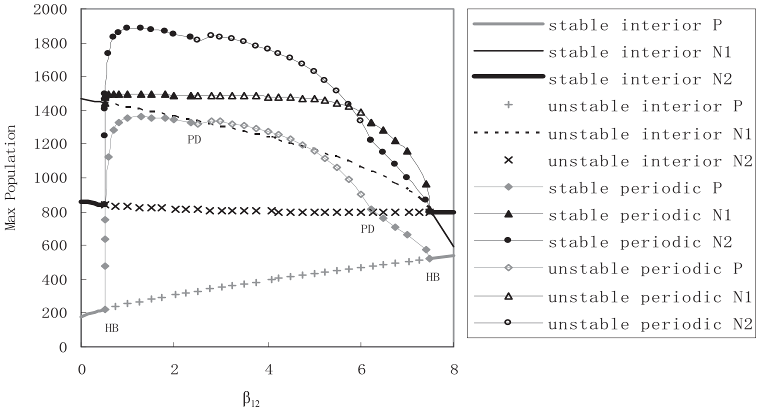

FIGURE 4. A bifurcation diagram calculated using AUTO. It shows that a stable interior equilibrium exists for either small or large β_{12} (solid lines). It identifies two Hopf bifurcation points (HB) and two period-doubling bifurcation points (PD). The symbols ▲ , ●, ♦ represent the maximum of the stable periodic solutions, while symbols $\triangle$, $\circ$, and $\diamond$ represent the maximum of the stable period-doubling solutions. The parameter values used are: r_1=0.00167, r_2=0.0028, K_1=50000, K_2=150000, β_{21}=2.5, e_1=0.0001, e_2=0.0005, $h_1=\dfrac{1}{16}$, $h_2=\dfrac{1}{200}$, G_1=8, G_2=100, B_1=0.00001, B_2=0.000056, D=0.000114.

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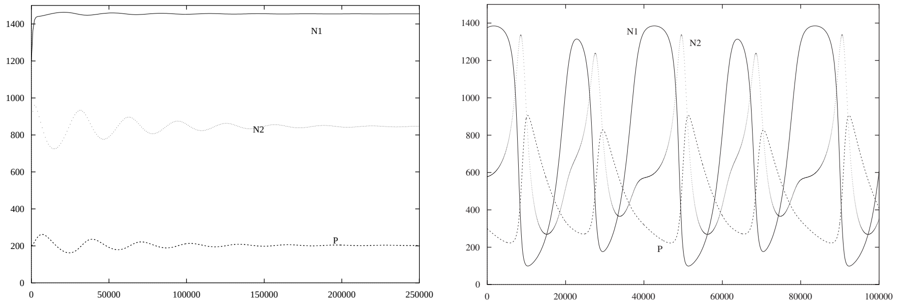
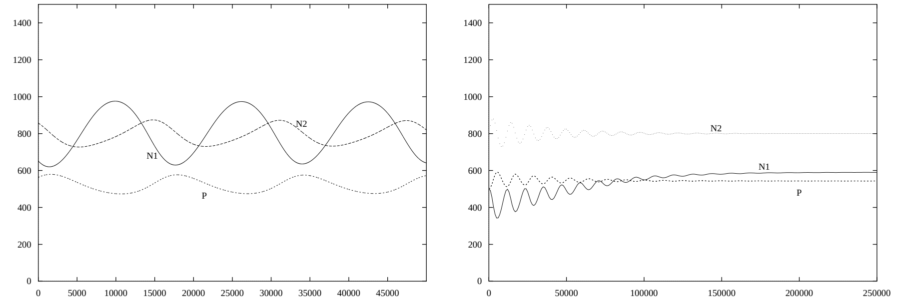


(a) $\beta_{12} \times 10^5 = 0.3$ (b) $\beta_{12} \times 10^5 = 6$



(c) $\beta_{12} \times 10^5$=7.4 (d) $\beta_{12} \times 10^5$=8

FIGURE 5. Time plots for various values of β_{12} chosen according to the diagram in Fig. 4. The population densities of P, N_1 and N_2 have been rescaled.

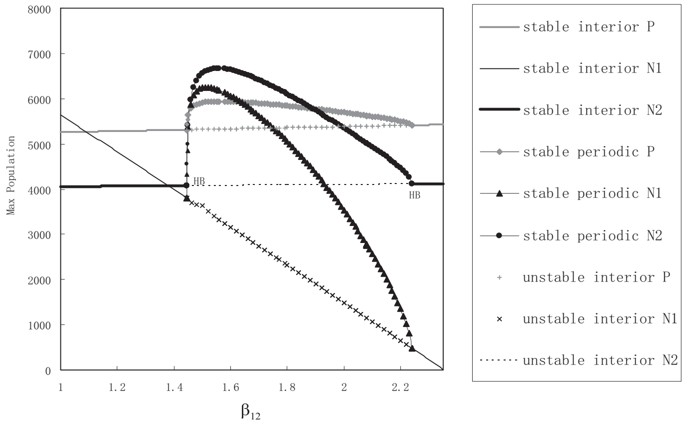
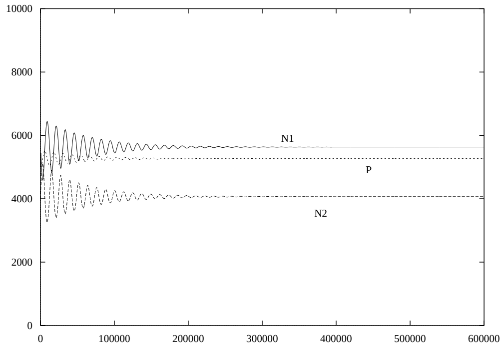
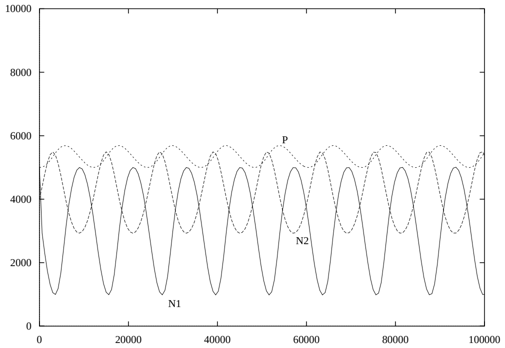


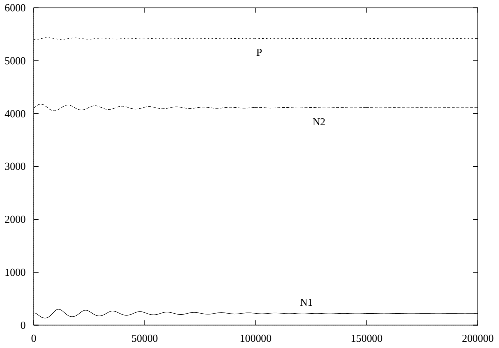
FIGURE 6. Similar to Fig. 4 except that this is for the case of $K_i < N_{im}$, $i = 1, 2$ (so that the functional response $g_i(N_1, N_2)$ is monotone for $0 < N_i < K_i$, $i = 1, 2$). All parameter values are the same as those in Fig. 4 except that r_1=0.0167, K_1=10000, K_2=100000, and β_{21}=1.1. It shows two Hopf bifurcation points (HB) but no period-doubling bifurcation.



(a) $\beta_{12} \times 10^5$=1.2



(b) $\beta_{12} \times 10^5$=1.6



(c) $\beta_{12} \times 10^5$=2.3

FIGURE 7. Similar to Fig. 5 except that the various values of β_{12} are chosen according to the diagram in Fig. 6. The β_{12} values for Fig. 7 (a) and (c) are chosen from intervals in which the interior equilibrium is stable, while the β_{12} value for Fig. 7 (b) is in the interval in which a stable periodic solution exists. The parameter values used are the same as those in Fig. 6.