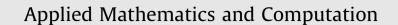
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## Dynamical behavior of a food chain model with prey toxicity



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#### ABSTRACT

This paper deals with a three-dimensional plant-herbivore-predator model that incorporates explicitly the plant toxicity in plant-herbivore interactions. The existence and stability conditions of all the feasible equilibria are established. Our results indicate that plant toxicity may play a key role in the dynamical behavior of the system. By adding another plant species with a different toxicity level to this system, we derive threshold conditions on the invasion of the second plant species. The analysis indicates that several parameters may be critical to determine successful invasion. Numerical simulations are also provided to reinforce the theoretical conclusions.

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#### 1. Introduction

Food chain models are often used in ecology to study the interactions of species with each other, which gives insight on the dynamics of populations of species. Among all the food chain models in natural ecosystems, plant–herbivore–predator interactions are the most essential. Scientists have employed functions such as Holling type II [1,2], Hassell–Varley [3] and Michaelis–Menten functional response [4] in their models, and studied in detail the rich dynamical behaviors of the systems. For the past several years, the chemically mediated plant–herbivore interactions have become the focus of intensive research in ecology, evolutionary biology and resource management [5–8]. Research on herbivores suggested that plant toxins play an important role in regulating herbivores' consumption of the plant [8–12]. Therefore, we established a toxin-induced herbivory functional response in [13], based on the traditional Holling type II function. Analytical results showed that plant toxins played a key role in the dynamical behaviors of plant–herbivore interactions.

To see clearly how plant toxins and predation may alter the plant-herbivore-predator interactions, we consider a threespecies food chain system in this paper. The system is composed of plant (prey), herbivore (predator) and carnivore (top predator). The toxin-determined functional response in [13] is employed to model plant-herbivore interactions. Both extinction and coexistence conditions are established for this system. By choosing proper bifurcation parameters, we develop threshold criteria for Hopf bifurcation. Moreover, in order to study the complex interactions between plant species, we extend the model to a 4-dimensional system by adding another plant species that contains toxins. The two species compete for the same nutrient resource. We focus on the conditions when the second species can invade the system successfully.

The paper is organized as follows. In Section 2, we introduce the three-dimensional food chain model. Section 3 deals with the existence and stability of all possible equilibria. In order to explore how plant toxins affect the system, *G* is chosen as the bifurcation parameter. The numerical simulations of the model are also provided. In Section 4, we establish the threshold conditions on the invasion of the second plant species. Two scenarios are considered here: invasion from steady states

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http://dx.doi.org/10.1016/j.amc.2014.05.088 0096-3003/© 2014 Elsevier Inc. All rights reserved. and invasion from limit cycles. Theoretical results indicate that successful invasion may be affected by several parameters such as plant toxicity, competition intensity and growth rate of plants. Section 5 contains a general discussion of the model and biological implications of our mathematical conclusions.

#### 2. Model description

Let S(t), P(t) and  $N_1(t)$  be the population densities of the carnivore (predator), the herbivore and the plant species, respectively. The consumption rate of the predator is modeled by the traditional Holling type II functional response

$$f(P)=\frac{eP}{1+heP},$$

where e stands for the encounter rate of herbivores, h is the handling time of per herbivore. As for the herbivore, We employ the toxin-determined consumption rate of [13], which is defined by

$$g(N_1) = \frac{e_1 N_1}{1 + \tilde{h}_1 e_1 N_1}$$

In the above expression,  $e_1$  represents the encounter rate per unit of plant,  $\tilde{h}_1$  is the toxin-mediated handling time. It is expressed as

$$\tilde{h}_1 = \begin{cases} \frac{h_1}{1-\alpha_1 e_1 N_1/G_1}, & \alpha_1 e_1 N_1 < G_1; \\ \infty, & \alpha_1 e_1 N_1 \geqslant G_1. \end{cases}$$

It follows that

$$g(N_1) = \begin{cases} \frac{e_1 N_1 (1 - \alpha_1 e_1 N_1 / G_1)}{1 - \alpha_1 e_1 N_1 / G_1 + h_1 e_1 N_1}, & \alpha_1 e_1 N_1 < G_1; \\ 0, & \alpha_1 e_1 N_1 \ge G_1. \end{cases}$$
(1)

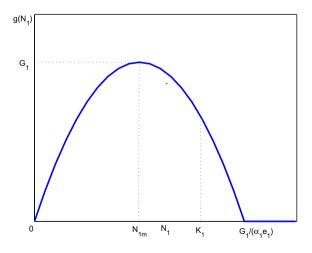
 $G_1$  denotes the toxin-adjusted maximal amount of plant a herbivore can ingest per unit time,  $h_1$  is the handling time of plant without toxicity. As  $\frac{1}{h_1}$  is the maximum intake rate in the absence of toxins, we assume  $G_1 < \frac{1}{h_1}$ .  $\alpha_1$  is a scaling parameter. It is easy to show that  $g(N_1)$  first increases to its maximum at

$$N_{1m}=\frac{G_1}{e_1\left(\sqrt{\alpha_1h_1G_1}+\alpha_1\right)},$$

then it decreases to zero. The constraint  $g(N_{1m}) = G_1$  requires

$$\alpha_1 = \left(1 - \sqrt{h_1 G_1}\right)^2.$$

A more biologically reasonable scenario is that  $N_{1m}$  is much smaller than  $K_1$ . Therefore, we assume  $\alpha_1 e_1 K_1 < G_1$  and  $N_{1m} < K_1$  in the remainder of this paper. The graph of  $g(N_1)$  is shown in Fig. 1.



**Fig. 1.** The toxin-determined functional response  $g(N_1)$ .

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