Dynamics of a plant–herbivore–predator system with plant-toxicity

Zhilan Feng a, Zhipeng Qiu b, Rongsong Liu c, Donald L. DeAngelis d,⇑

a Department of Mathematics, Purdue University, West Lafayette, IN 47907, USA
b Department of Applied Mathematics, Nanjing University of Science and Technology, Nanjing 210094, PR China
c Department of Mathematics, University of Wyoming, Laramie, WY 82071, USA
d US Geological Survey, Florida Integrated Science Center and Department of Biology, University of Miami, Coral Gables, FL 33124, USA

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A system of ordinary differential equations is considered that models the interactions of two plant species, populations, an herbivore population, and a predator population. We use a toxin-determined functional response to describe the interactions between plant species and herbivores and use a Holling Type II functional response to model the interactions between herbivores and predators. In order to study how the predators impact the succession of vegetation, we derive invasion conditions under which a plant species can invade into an environment in which another plant species is co-existing with a herbivore population with or without a predator population. These conditions provide threshold quantities for several parameters that may play a key role in the dynamics of the system. Numerical simulations are conducted to reinforce the analytical results. This model can be applied to a boreal ecosystem trophic chain to examine the possible cascading effects of predator-control actions when plant species differ in their levels of toxic defense.

1. Introduction

Plant–herbivore–predator interactions are important in all ecosystems. However, their complexity is such that these interactions are still only partially understood. Mathematical modeling has provided a very useful tool for understanding complex dynamics of ecosystems. A key component in modeling herbivore–plant interactions is the herbivore’s functional response [15], which can link herbivory to plant populations. The functional response is the instantaneous change in the rate of prey (plant) intake by a predator (herbivore) in response to changing prey biomass. The most commonly used functional response is the Holling Type II response, which is characterized by a monotonic increase in intake, asymptoting towards a maximum rate of biomass consumption.

Traditional functional response models specialized to mammalian browsing (e.g., [1, 9, 14, 23, 24, 29, 32]), however, do not include explicitly the effect of plant toxicity on plant–herbivore interactions. But many plants are heavily defended against herbivory by secondary chemicals, and in many mammal–plant interactions these toxins determine satiation (reviewed by [5, 10, 13, 26, 31]). Research on herbivores indicates that aversion to toxic plants (conditioned food aversions) can occur in large domestic animals (e.g., [31]) and other herbivores [10]. The implications for plant and herbivore populations and community dynamics of plant defenses have been explored to only a small extent.

Because plants vary in toxicity, mammalian herbivores feed selectively (see reviews by [5, 10, 13, 26, 31]). This selectivity affects plant succession and vegetation diversity, ultimately affecting ecosystem processes such as nutrient cycling (e.g., [3, 4, 6, 7, 8, 18, 19, 27, 28]). However, the mechanisms by which toxin-mediated selective herbivory affects vegetation are unclear. To fill this vacuum we have begun constructing a toxin-determined functional response model (acronym TDFRM) of plant–mammal interactions [11, 12, 21, 22, 33].

The toxin-determined functional response in Li et al. [21] is a modification of the traditional Holling Type 2 response to include the negative effect of toxin on herbivore growth, which can overwhelm the positive effect of biomass ingestion at sufficiently high plant toxicant concentrations. In Feng et al. [11] and Liu et al. [22], we compared the qualitative properties of the TDFRM and the Holling Type 2 functional response model (acronym H2FRM). The results show that the difference in the functional responses can lead to dramatically different outcomes, summarized in the bifurcation diagram (see Fig. 5 in [22]), and that a wide variety of dynamics may occur due to the interplay of Holling Type 2 dynamics and the effect of the plant toxicant. These dynamics include the occurrence of bistability, in which both a periodic solution and the herbivore-extinction equilibrium are attractors, as well the possibility of a homoclinic bifurcation. In Feng et al. [11], we parameterized the models for the Tanana Floodplain system and computed

⇑ Corresponding author. Address: Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA.
E-mail address: ddeangelis@bio.miami.edu (D.L. DeAngelis).