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MATHEMATICAL MODELS OF PLANT-HERBIVORE INTERACTIONS

Zhilan Feng and Donald L. DeAngelis

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Mathematical Models of Plant-Herbivore Interactions

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I dedicate this book to my daughter Haiyun and my son Henry for all your love and support
–Zhilan Feng

I thank my wife Lie for her love and patience
–Donald L. DeAngelis

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Foreword

In the latter half of the twentieth century, research directed toward obtaining a mechanistic understanding of the causes and effects of plant anti-herbivore defense became the focus of intense research in ecology and evolution. Part of this research effort has been the development of a diverse set of mathematical models of these mechanisms. The intent of this book is to introduce and summarize the current state of these modeling efforts. Professor Feng and Dr. DeAngelis have admirably achieved this.

This book begins with a sound introduction to basic mathematical theories of general predator-prey interactions such as the Rosenzweig–MacArthur equations. This introduction is followed by consideration of how these equations have been used to mathematically analyze interactions between plants and their herbivore predators. Then more recent mathematical models of plant herbivore interactions, such as linear programming models, are discussed, and in this introduction the notion of plant chemical anti-herbivore defense is introduced. Following the introduction into mathematical models of the idea that plant chemical defenses could constrain herbivore attack of plants, a more recent set of models is introduced. These are based upon the effects that plant toxins could have on the functional response of herbivores to plant biomass. This toxin-determined functional response model (the TDFRM), which has been successfully tested at least once in a long-term ecological research project, provides a potentially very powerful theoretical basis for plant chemical defense theory, especially as it applies to generalist herbivores such as browsing mammals.

The TDFRM is founded upon two observations that I made in Alaska over forty years ago. The first observation was on winter browsing mammals such as the snowshoe hare (*Lepus americanus*), the moose (*Alces alces gigas*), and ptarmigan (*Lagopus* spp.). These fed preferentially upon woody plant species, the ontogenetic stages (juvenile versus mature) of these species, and parts of the twigs of ontogenetic stages that were not rich in lipid-soluble substances that were potentially toxic. They tended to avoid eating much of the biomass of species, ontogenetic stages, and twig parts that were comparatively rich in these potential toxins. This observation suggested that the browsing mammals that I was familiar with were attempting to minimize toxin intake. The second observation was that, when a generally little-browsed species that was rich in lipid-soluble toxins, such as the Siberian green alder (*Alnus viridis* subsp. *fruitcosa*), occurred in low biomass in a forest patch, snowshoe hares browsed it to an extraordinarily high degree. I could come up with only one explanation for this observation: Even though an individual snowshoe hare could eat only a few grams of the twig biomass of green alder, if the biomass of green alder was a relatively small fraction of the forest vegetation and multiple hares each fed on the few green alder plants available to them, the combined effect of numerous hares would result in severe browsing of the few green alders. But, if the biomass of green alder was greater and the biomass of hares was constant, then, as generally observed, green alder would be lightly browsed. This observation again suggested that toxins, in this case the stilbenes pinosylvin and pinosylvin mono-methyl ether of green alder, were regulating the rate at which the herbivores, in this case snowshoe hares, were eating the biomass of their prey. If this was the case, then the rate of intake of green alder biomass by snowshoe hares could be modeled as some sort of Michaelis–Menten function in which detoxification processes were controlling the herbivore's rate of predation on its plant prey. Subsequent experiments using snowshoe hares and a toxic defense of the juvenile stage of the Alaska paper birch (*Betula neoalaskana*), the dammarane triterpene papyriferic acid, strongly supported this hypothesis.

With this information in hand, I was fortunate enough to meet with Professor Feng and to mention this possibility to her. Professor Feng immediately suggested that a good way to mathematically describe what I explained to her was to add a term to C. S. Holling's functional response predator-prey model that enabled toxicity to regulate the intake of plant biomass by a generalist herbivore. This was the beginning of the TDFRM theory developed in later chapters of this book. Subsequent to the building of the initial TDFRM, the effects of predators of herbivores such as wolves in a tritrophic system were developed, and the results of this extension now appear to accurately predict the dynamics of a woody plant-moose-wolf system in interior Alaska. Additionally, the notion of herbivore evasion of their predators has been coupled to the initial TDFRM, and this coupling could well provide a powerful tool in analyzing the "landscape of fear" hypothesis that predicts that, at the level of the landscape, toxin-determined foraging and the fear of predation interact to determine the foraging behavior of herbivores.

So, to summarize, this book begins with an excellent introduction of predator-prey theory as it applies to plant-herbivore interactions and ends with what now appears to be a powerful mathematical model of how plant toxins affect the dynamics of these interactions at levels extending from individual plant parts and individual herbivores to tritrophic interactions across entire landscapes.

John P. Bryant

Cora, Wyoming (Institute of Arctic Biology, University of Alaska Fairbanks, retired)

Preface

This book arose out of a long collaboration between the authors on attempting to use mathematical modeling to describe and understand the effects that plant defenses have on plant-herbivore dynamics. The core of the book involves a toxin-determined functional response model (the TDFRM) that was formulated with specific reference to mammalian browsers in the boreal forest confronted with plant communities in which species could have varying degrees of defense. This model and its elaborations itself spans a great range of dynamic behaviors. However, we felt it was not enough to constitute a complete book. Therefore, we have expanded the book both to include other plant-herbivore work we have been involved with and to provide an even broader context of modeling plant-herbivore interactions.

The book is divided into two halves, one a mathematical overview and the other selected applications. We begin in Chapter 1 with a very general conceptual overview of the modeling of plant growth and resource allocation, as well as of herbivore foraging, and then briefly review the resultant plant-herbivore interactions. Chapter 2 derives the basic Holling type 2 functional response and some of the general properties of predator-prey interactions with the functional response. In Chapter 3, well-known ecological models are used to illustrate five key concepts in herbivore-plant interactions. The TDFRM is described in detail in Chapter 4, including extension to spatial situations.

The applied half of the book begins with models related to a plant's dealing with herbivory, both through allocation of energy to inducible defenses and its ability to compensate for various levels of herbivory (Chapter 5). In Chapter 6, the emphasis is on herbivores' foraging strategies in response to the problems posted by low plant quality (low nutrient concentration) toxins, and predators. The use of the TDFRM to describe effects of toxicity at the food chain and ecosystem levels is covered in Chapter 7. In Chapter 8, we try to provide a broader conceptual view of how the prevalence of fire is related to the strong presence of plant toxicity in the boreal biome and how this shapes species distributions. Chapter 9 is a primer on the use of *Mathematica* in simulating the models described here. Particularly, we demonstrate the feature that allows the simultaneous visualization of model outcomes as parameter values are varying, which is especially useful for decision making in management.

This book is intended for graduate students and others who have some background in nonlinear differential equations, but we hope that the material in Chapters 2 and 3 is a relatively easy introduction that will make the rest of the book accessible to many readers. The book is not intended to be a complete textbook, as the topics by no means cover all the vast field of modeling of plant-herbivore interactions but to some extent reflect both the authors' primary experience with mammal browsers in the boreal forest. Also, we have generally avoided large, complex simulation models in favor of mathematical models of moderate complexity. But many of the key ways that nonlinear differential equations are used to describe plant-herbivore interactions are represented here.

We are indebted to our many collaborators on earlier works and publications, some of which are represented here. The TDFRM initially was developed as a collaboration between John Bryant, Zhilan Feng, and Robert Swihart, motivated by John's conjectures based on

field observations and experiences in real ecological systems. This collaboration was later joined by Donald DeAngelis and Rongsong Liu. An NSF grant that supported this project (DMS-0920828) helped to establish the collaboration with a team from the University of Alaska in Fairbanks, including F. Stuart Chapin III, Tim Glaser, Knut Kielland, Mark Olson, and Jennifer Schmidt, and to provide support for students at Purdue University including Jorge Alfaro-Murillo, Matthew Barga, Muhammad Hanis B. Ahamad Tamrin, and Yiqiang Zheng. The inducible defense modeling described in Chapter 5 was the result of a collaboration of DeAngelis and a team of empiricists and modelers led by Matthijs Vos. The snowshoe hare dynamics modeling was done with Rongsong Liu, Stephen Gourley, and John Bryant. A model of plant compensation was the work of DeAngelis with Shu Ju. Some of the results for the TDFRM described in Chapters 4 and 7 involved collaborations of DeAngelis and Feng with Carlos Castillo-Chavez, Xiuli Cen, Wenzhang Huang, Ya Li, Zhipeng Qiu, and Yulin Zhao.

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Part I

Basic Theory and Simple Models

Chapter 1

Introduction

1.1 Types of plant-herbivore interactions; e.g., plant and herbivore diversity, types of herbivore feeding on plants

The interaction between herbivores and plants is one of the most fundamental processes in ecology and has been the object of scientific observation and theory as early as Aristotle [352], but mathematical modeling has been applied to plant-herbivore interactions for only a few generations. The earliest mathematical models in ecology were the so-called predator-prey models of Lotka [230] and Volterra [371]. These are models described by differential equations for both populations, including terms reflecting the rate of predation of the predator on the prey, and in which the variables could be either population numbers or biomasses. Lotka–Volterrra models could describe in a qualitative way the sort of periodic oscillations that were sometimes observed in nature in terms of predator-prey interactions.

Over time many variations on the initial Lotka–Volterra equations have been proposed and analyzed to try to better understand population interactions. With little change, these predator-prey models have been adapted to describe the special class of predator-prey interactions between plants and herbivores. (The term "predator-prey" is probably not a good one for these interactions, as it conjures up an image of a predator chasing prey individuals, which does not fit herbivore-plant interactions. But we will use the term in places where general interactions are meant.)

Both theory and modeling of plant-herbivore systems have extended far beyond the simple interactions of the Lotka–Volterra type to encompass a whole range of aspects of such interactions, and these continuous-time models have been joined by discrete-time difference equation models. Even to attempt to list the manifold types of models devoted to plant-herbivore interactions would be difficult, but some sort of categorization is needed. As a first cut, Caughley and Lawton [55] divided plant-herbivore interactions into "non-interactive" and "interactive." The non-interactive type encompasses situations in which the feeding by the herbivore generally does not influence vegetation growth. Herbivory on seeds or fruits would fall into this category. Even though frugivory and seed predation can remove biomass from the plant, they do not influence the plant growth rate the way removal of foliage and roots does. Non-interactive herbivory is important ecologically, as it sustains many animal species, but it is less interesting from a mathematical standpoint than when the herbivory is interactive.

Interactive herbivory refers to situations where the rate of change of herbivore biomass depends on plant biomass and the rate of change of plant biomass depends on herbivore