

Chapman & Hall/CRC
Mathematical and Computational Biology Series

MATHEMATICAL MODELS OF PLANT-HERBIVORE INTERACTIONS

Zhilan Feng and Donald L. DeAngelis



CRC Press
Taylor & Francis Group

A CHAPMAN & HALL BOOK

Mathematical Models of Plant-Herbivore Interactions

CHAPMAN & HALL/CRC

Mathematical and Computational Biology Series

Aims and scope:

This series aims to capture new developments and summarize what is known over the entire spectrum of mathematical and computational biology and medicine. It seeks to encourage the integration of mathematical, statistical, and computational methods into biology by publishing a broad range of textbooks, reference works, and handbooks. The titles included in the series are meant to appeal to students, researchers, and professionals in the mathematical, statistical and computational sciences, fundamental biology and bioengineering, as well as interdisciplinary researchers involved in the field. The inclusion of concrete examples and applications, and programming techniques and examples, is highly encouraged.

Series Editors

N. F. Britton

*Department of Mathematical Sciences
University of Bath*

Xihong Lin

*Department of Biostatistics
Harvard University*

Nicola Mulder

*University of Cape Town
South Africa*

Maria Victoria Schneider

European Bioinformatics Institute

Mona Singh

*Department of Computer Science
Princeton University*

Anna Tramontano

*Department of Physics
University of Rome La Sapienza*

Proposals for the series should be submitted to one of the series editors above or directly to:

CRC Press, Taylor & Francis Group

3 Park Square, Milton Park
Abingdon, Oxfordshire OX14 4RN
UK

Published Titles

An Introduction to Systems Biology: Design Principles of Biological Circuits

Uri Alon

Glycome Informatics: Methods and Applications

Kiyoko F. Aoki-Kinoshita

Computational Systems Biology of Cancer

*Emmanuel Barillot, Laurence Calzone,
Philippe Hupé, Jean-Philippe Vert, and
Andrei Zinovyev*

Python for Bioinformatics, Second Edition

Sebastian Bassi

Quantitative Biology: From Molecular to Cellular Systems

Sebastian Bassi

Methods in Medical Informatics: Fundamentals of Healthcare Programming in Perl, Python, and Ruby

Jules J. Berman

Chromatin: Structure, Dynamics, Regulation

Ralf Blossey

Computational Biology: A Statistical Mechanics Perspective

Ralf Blossey

Game-Theoretical Models in Biology

Mark Broom and Jan Rychtář

Computational and Visualization Techniques for Structural Bioinformatics Using Chimera

Forbes J. Burkowski

Structural Bioinformatics: An Algorithmic Approach

Forbes J. Burkowski

Spatial Ecology

*Stephen Cantrell, Chris Cosner, and
Shigui Ruan*

Cell Mechanics: From Single Scale- Based Models to Multiscale Modeling

*Arnaud Chauvière, Luigi Preziosi,
and Claude Verdier*

Bayesian Phylogenetics: Methods, Algorithms, and Applications

Ming-Hui Chen, Lynn Kuo, and Paul O. Lewis

Statistical Methods for QTL Mapping

Zehua Chen

An Introduction to Physical Oncology: How Mechanistic Mathematical Modeling Can Improve Cancer Therapy Outcomes

*Vittorio Cristini, Eugene J. Koay,
and Zihui Wang*

Normal Mode Analysis: Theory and Applications to Biological and Chemical Systems

Qiang Cui and Ivet Bahar

Kinetic Modelling in Systems Biology

Oleg Demin and Igor Goryanin

Data Analysis Tools for DNA Microarrays

Sorin Draghici

Statistics and Data Analysis for Microarrays Using R and Bioconductor, Second Edition

Sorin Drăghici

Computational Neuroscience: A Comprehensive Approach

Jianfeng Feng

Mathematical Models of Plant-Herbivore Interactions

Zhilan Feng and Donald L. DeAngelis

Biological Sequence Analysis Using the SeqAn C++ Library

Andreas Gogol-Döring and Knut Reinert

Gene Expression Studies Using Affymetrix Microarrays

Hinrich Göhlmann and Willem Talloen

Handbook of Hidden Markov Models in Bioinformatics

Martin Gollery

Meta-analysis and Combining Information in Genetics and Genomics

Rudy Guerra and Darlene R. Goldstein

Differential Equations and Mathematical Biology, Second Edition

D.S. Jones, M.J. Plank, and B.D. Sleeman

Knowledge Discovery in Proteomics

Igor Jurisica and Dennis Wigle

Introduction to Proteins: Structure, Function, and Motion

Amit Kessel and Nir Ben-Tal

Published Titles (continued)

RNA-seq Data Analysis: A Practical Approach

*Eija Korpelainen, Jarno Tuimala,
Panu Somervuo, Mikael Huss, and Garry Wong*

Introduction to Mathematical Oncology

*Yang Kuang, John D. Nagy, and
Steffen E. Eikenberry*

Biological Computation

Ehud Lamm and Ron Unger

Optimal Control Applied to Biological Models

Suzanne Lenhart and John T. Workman

Clustering in Bioinformatics and Drug Discovery

John D. MacCuish and Norah E. MacCuish

Spatiotemporal Patterns in Ecology and Epidemiology: Theory, Models, and Simulation

*Horst Malchow, Sergei V. Petrovskii, and
Ezio Venturino*

Stochastic Dynamics for Systems Biology

Christian Mazza and Michel Benaïm

Statistical Modeling and Machine Learning for Molecular Biology

Alan M. Moses

Engineering Genetic Circuits

Chris J. Myers

Pattern Discovery in Bioinformatics: Theory & Algorithms

Laxmi Parida

Exactly Solvable Models of Biological Invasion

Sergei V. Petrovskii and Bai-Lian Li

Computational Hydrodynamics of Capsules and Biological Cells

C. Pozrikidis

Modeling and Simulation of Capsules and Biological Cells

C. Pozrikidis

Cancer Modelling and Simulation

Luigi Preziosi

Introduction to Bio-Ontologies

Peter N. Robinson and Sebastian Bauer

Dynamics of Biological Systems

Michael Small

Genome Annotation

*Jung Soh, Paul M.K. Gordon, and
Christoph W. Sensen*

Niche Modeling: Predictions from Statistical Distributions

David Stockwell

Algorithms for Next-Generation Sequencing

Wing-Kin Sung

Algorithms in Bioinformatics: A Practical Introduction

Wing-Kin Sung

Introduction to Bioinformatics

Anna Tramontano

The Ten Most Wanted Solutions in Protein Bioinformatics

Anna Tramontano

Combinatorial Pattern Matching Algorithms in Computational Biology Using Perl and R

Gabriel Valiente

Managing Your Biological Data with Python

*Allegra Via, Kristian Rother, and
Anna Tramontano*

Cancer Systems Biology

Edwin Wang

Stochastic Modelling for Systems Biology, Second Edition

Darren J. Wilkinson

Big Data Analysis for Bioinformatics and Biomedical Discoveries

Shui Qing Ye

Bioinformatics: A Practical Approach

Shui Qing Ye

Introduction to Computational Proteomics

Golan Yona

Mathematical Models of Plant-Herbivore Interactions

Zhilan Feng
Donald L. DeAngelis



CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

A CHAPMAN & HALL BOOK

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

© 2018 by Taylor & Francis Group, LLC
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works

Printed on acid-free paper
Version Date: 20170719

International Standard Book Number-13: 978-1-4987-6917-4 (Hardback)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access www.copyright.com (<http://www.copyright.com/>) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

Trademark Notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

Visit the Taylor & Francis Web site at
<http://www.taylorandfrancis.com>

and the CRC Press Web site at
<http://www.crcpress.com>

*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



Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

Contents

Foreword	xiii
Preface	xv
List of Figures	xvii
List of Tables	xix
I Basic Theory and Simple Models	1
1 Introduction	3
1.1 Types of plant-herbivore interactions; e.g., plant and herbivore diversity, types of herbivore feeding on plants	3
1.2 Plant growth and allocation	5
1.3 Modeling herbivore foraging strategies	6
1.4 The consequences of herbivore-plant interactions	8
2 Predator-Prey Interactions	11
2.1 Beginnings of predator-prey modeling	11
2.2 Derivation of the Holling type 2 and type 3 functional responses	13
2.3 Incorporating the predator functional response into one-predator and one-prey equations	16
2.3.1 Equilibria of the one-prey one-predator system	18
2.4 Functional response for predation on two or more prey species	19
2.5 Stability of model equilibria	20
3 Overview of Some Results of Plant-Herbivore Models	23
3.1 Introduction	23
3.1.1 Non-interactive	23
3.1.2 Interactive	24
3.2 The theory of top-down control	24
3.3 Paradox of enrichment	28
3.4 Collapse of a grazer-plant system	31
3.5 Herbivore outbreaks	34
3.6 Effects of plant quality	38
3.7 Glossary	41

4	Models with Toxin-Determined Functional Response	43
4.1	A simple TDFRM with a single plant population	44
4.1.1	Derivation and emerging properties of the model	45
4.1.2	Dynamics for constant browsing preference	46
4.1.2.1	Bifurcation analysis	47
4.1.3	Dynamics for non-constant browsing preference	54
4.1.4	Global dynamics of the 2-dimensional TDFRM	55
4.2	A 3-dimensional TDFRM with two plant species	59
4.2.1	The model with two plant species	60
4.2.2	Validation of the model	61
4.2.3	Analytic results for fixed allocation of foraging effort σ_i	64
4.2.3.1	Analysis of the model in the absence of toxins	65
4.2.3.2	Analysis of the model with toxins included	65
4.2.4	Adaptive foraging by adjusting feeding effort $\sigma_i(t)$	66
4.3	Plant-herbivore interactions with age-dependent toxicity	72
4.3.1	The model with age-dependent toxicity	73
4.3.2	Herbivore extinction and oscillations	75
4.4	Reaction-diffusion modeling approach	77
4.4.1	A 2-D TDFRM with herbivore movement included	78
4.4.2	Existence of traveling wave solutions	81
4.5	Glossary	85
II	Applications	87
5	Plant Quality and Plant Defenses: Parallels and Differences	89
5.1	Induced defense in plants: Effects on plant-herbivore interactions	89
5.1.1	Introduction	89
5.1.2	Model 1	91
5.1.3	Model 2	97
5.2	Plant defense allocation strategies	105
5.2.1	Allocation of resources by plants	106
5.2.2	Allocation when anti-herbivore defenses are included	107
5.2.2.1	PLATHO model	109
5.2.3	Methods of compensation for herbivore damage	111
5.2.3.1	Model of plant compensation	112
5.2.3.2	Deriving a function for the optimization of G	114
5.2.3.3	Numerical evaluation of G as a function of allocations η_f , η_r , and η_w	115
5.3	Glossary	116
6	Herbivore Strategies: The Role of Plant Quality and Defenses	119
6.1	Herbivore strategies in exploiting plants	119
6.1.1	Introduction	119
6.1.1.1	Food quality	120
6.1.1.2	Plant defenses	120
6.1.2	Herbivore adaptations	120
6.1.3	Modeling feeding choice to optimize intake of a limiting nutrient	121
6.1.4	Constraint on plant toxin intake	124

6.1.5	An herbivore foraging on spatially distinct patches	124
6.1.6	Linear programming to determine optimal selection of plant types	127
6.2	Snowshoe hares browsing strategy in the presence of predator	129
6.2.1	Vegetation-hare-generalist predator model	130
6.2.2	Vegetation-hare-specialist predator model	133
6.3	Glossary	137
7	Plant Toxins, Food Chains, and Ecosystems	139
7.1	A plant toxin mediated mechanism for the lag in snowshoe hare dynamics	139
7.1.1	Application of the model to the shrub birch <i>Betula glandulosa</i>	142
7.1.2	Experiments	143
7.1.3	Model predictions	146
7.1.4	Discussion	148
7.2	Dynamics of the TDFRM with plant, herbivore, and predator	150
7.2.1	Invasion criterion of toxic plant in an equilbrial environment	153
7.2.2	Invasion criterion of toxic plant in an oscillatory environment	157
7.3	Applications of TDFRM to a boreal forest landscape	159
7.3.1	Integration of TDFRM and ALFRESCO	161
7.3.2	Plant toxins and trophic cascades alter fire regime and succession on a boreal forest landscape	164
7.3.3	More on the integration of TDFRM and ALFRESCO	166
7.3.3.1	Parameter estimation and calibration	169
7.3.4	Discussion	172
7.4	Glossary	173
8	Fire, Herbivory, Tree Chemical Defense, and Spatial Patterns in the Boreal Forest	175
8.1	Introduction	175
8.2	Fire's relationship to browsing mammal abundance	175
8.3	Antibrowsing chemical defenses of <i>B. neoalaskana</i> and <i>B. papyrifera</i> : Benefit and cost	176
8.4	Fire's relationship to the distributions of <i>B. neoalaskana</i> and <i>B. papyrifera</i>	179
9	Example of <i>Mathematica</i> Notebooks	183
9.1	Simulations of a simple plant-herbivore model	183
9.2	Sample codes for simulations of TDFRM	185
9.3	Plots of stochastic simulations for spatial distributions of vegetation	187
9.4	<i>Mathematica</i> notebooks	189
	References	193
	Index	217



Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

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. *fruticosa*), 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.

List of Figures

1.1	Plant-herbivore responses	4
2.1	Predator movement	14
2.2	Diagram of predator-prey state plane	18
3.1	Three trophic level food chain	26
3.2	Four trophic level food chain	27
3.3	Zero isoclines of equations (3.2a,b)	29
3.4	Zero isoclines of equations (3.4a,b)	31
3.5	Close-up of state plane with equilibrium point left of peak	31
3.6	Oscillations of the system described by equations (3.2a,b)	32
3.7	Plots of $C(P)$ and $G(P)$	34
3.8	Plot of $G(P)$ for different values of H_0	35
3.9	Plots of both sides of equation (3.13) as functions of μ	37
3.10	Bifurcation diagram in (R, Q) -space	38
3.11	Plots of simulations of system (3.14a,b)	40
3.12	Bifurcation diagram as K is increased	41
4.1	Graph of the functional response $C(P)$ given in (4.2)	47
4.2	Plot of the function $g(P)$	48
4.3	Intersections of the curve $C(P)$ with the line d/B	49
4.4	Bifurcation diagram for the 2-D TDFRM with constant σ	50
4.5	$H = g(P)$ and stability of equilibria	51
4.6	Phase portraits of the 2-D TDFRM with constant σ	52
4.7	Numerical simulations of the 2-D TDFRM	53
4.8	Bifurcation diagram of the 2-D TDFRM for non-constant σ	55
4.9	Vector field of system (4.21) with one or two equilibria	58
4.10	Global attraction regions of system (4.1)	58
4.11a	A closure experiment in Tanana at time $t = 0$ (1985)	62
4.11b	A closure experiment in Tanana at time $t = 8$	62
4.11c	A closure experiment in Tanana at time $t = 15$	63
4.11d	Outcomes of the closure experiment in Tanana	63
4.12	Comparison of simulations between TDFRM and HT2FRM	64
4.13	Diagram for species invasion	66
4.14	Dynamics of the 3-D HT2FRM with adaptive feeding	67
4.15	Dynamics of the 3-D TDFRM with adaptive feeding	68
4.16	Simulations of the 3-D TDFRM with $r_1 > r_2$ and $G_1 > G_2$	69
4.17	Similar to Figure 4.15 but for the case of $G_1 < G_2$	70
4.18	Plant toxicity and invasion	71
4.19	Simulation results under the interactive functional response $\tilde{C}_i(P_1, P_2)$	72
4.20	Numerical simulations of model (4.35) and dependence on τ_1 , r , G_1 , and G_2	76
4.21	The region Ω defined in (4.52)	82

5.1	Schematic diagram of Model 1 (5.1)	92
5.2	Plot of the functions $I(H)$ and $D(H)$	93
5.3	Dependence of equilibrium values on K for Model 1 without P_2	94
5.4	Response of equilibrium values P_1^* , P_2^* , and H^* to K for Model 1	95
5.5	Transcritical point K_{tc} and Hopf bifurcation point K_{Hopf}	96
5.6	Schematic diagram of Model 2	98
5.7	Changes in equilibrium of Model 2 as N_0 is increased	100
5.8	Similar to Figure 5.7 with and without switching	102
5.9	Transient behavior of model described in Figure 5.8	103
5.10	Invasion plot and a convergent ESS	104
5.11	Schematic of model for allocation of carbon and nutrient	112
5.12	Model outputs	117
6.1	Dependence of protein intake (NIR) on the number of plant types	123
6.2	Dependence of the maximum intake of protein on toxin limit	125
6.3	Fractions of encountered plant types the herbivore is able to ingest	126
6.4	Constraints on time for feeding, digestion, and energy intake need	128
6.5	Bifurcation diagrams of model (6.21) for vegetation and herbivore	133
6.6	Time plots of model (6.21) for vegetation and herbivores	135
6.7	Results of bifurcation analysis of model (6.24)	135
6.8	Dynamics for model (6.24) for $d_P = 1.0$	136
7.1	Twig of a woody plant before and after browsing by snowshoe hares	141
7.2	Conceptual diagram of biomass transfer among compartments	142
7.3	Results of the twig segment model (TSM) simulation	143
7.4	Results of the Kluane experiment	146
7.5	Number of solutions to $g(P_1) = H^*$ or $C(P_1) = d_h/B_1$	152
7.6	Stability switch of E_r^* as r_1 or G_1 varies	154
7.7	Bifurcation curves of the threshold quantity λ and time plots as $1/d_w$ or r_2 varies	156
7.8	Numerical solutions of the full system (7.1)	158
7.9	Stochastic factors included in ALFRESCO	162
7.10	Conceptual diagram for the integration of the TDFRM in the ALFRESCO	163
7.11	Stochastic simulations of spruce to deciduous ratio	165
7.12	Spatial stochastic simulations of vegetation coverage	166
7.13	Simulation results of the integrated TDFRM and ALFRESCO	167
8.1	The distributions of the Alaska resin birch <i>Betula neoalaskana</i> and the white birch <i>B. papyrifera</i>	177
8.2	The cost of antibrowsing defense	178
8.3	Locations of Dugle's collections of <i>B. neoalaskana</i> and <i>B. papyrifera</i>	180
8.4	Simulations of the 3-D TDFRM with different plant growth and toxicity	181
9.1	Simulation results of system (9.1) generated by Notebook I	184
9.2	Simulation results generated by Notebook II	185
9.3	Using the notebook II to compare control scenarios	186
9.4	Simulation results using notebook III with varying values of m_h	187
9.5	Spatially explicit stochastic simulations of vegetation dynamics	188

List of Tables

4.1	Local stability results when σ is constant.	52
4.2	Local stability results when $\sigma(P)$ is not constant.	55
4.3	Definition of parameters and values used in simulations.	75
5.1	Parameter values in Model 2 used in competition between plant populations with different values of g	105
5.2	Variables and parameters used in the model.	115
6.1	Parameter values for the model of Owen-Smith and Novellie [279].	123
7.1	Results of the Alaska experiment.	147
7.2	Peak snowshoe hare densities estimated in autumn.	150
7.3	Definition of parameters used in simulations. Sources for some of the pa- rameters are provided and the rest of the parameters were determined by calibration simulations.	171



Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

Part I

Basic Theory and Simple Models



Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

Chapter 1

Introduction

1.1	Types of plant-herbivore interactions; e.g., plant and herbivore diversity, types of herbivore feeding on plants	3
1.2	Plant growth and allocation	5
1.3	Modeling herbivore foraging strategies	6
1.4	The consequences of herbivore-plant interactions	8

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–Volterra 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