

Contents

Section I Introduction

1	The Various Effects of Insects on Ecosystem Functioning	3
	W.W. WEISSE and E. SIEMANN	
1.1	Summary	3
1.2	Introduction	3
1.3	A Brief Overview of Insect Effects on Ecosystem Function	8
1.3.1	Insect Effects on Ecosystem Function	
	Via Interactions with Plants	8
1.3.1.1	Herbivory	8
1.3.1.2	Plant-Insect Mutualisms	14
1.3.2	Other Direct and Indirect Effects of Insects on Ecosystem Function	14
1.4	The Aim and Structure of this Book	15
	References	19

Section II Insects and the Belowground System

2	Insect Herbivores, Nutrient Cycling and Plant Productivity	27
	S.E. HARTLEY and T. H. JONES	
2.1	Summary	27
2.2	Introduction	28
2.3	Decomposition	28
2.3.1	The Resources Available	28
2.3.2	Effects of Insect Herbivory on Decomposition	31

2.3.2.1	Herbivory and Litter Quality	31
2.3.2.2	Herbivory, Root Exudation and Root Biomass	32
2.4	Nutrient Cycling and Plant Productivity	33
2.4.1	Effects on Carbon and Nitrogen Cycling	34
2.4.1.1	Methane and Carbon Dioxide	34
2.4.1.2	Nitrogen and Phosphorus	35
2.4.1.3	Inputs from Aboveground Herbivores	36
2.4.1.4	The Importance of Belowground Biota: Evidence from Controlled Environment Studies	39
2.4.1.5	Insect Herbivory and Spatial Variation in Nutrient Availability	40
2.4.2	Herbivory and Plant Biomass	41
2.5	Conclusions	45
	References	46

3 **Indirect Effects of Invertebrate Herbivory
on the Decomposer Subsystem** 53

D.A. WARDLE and R.D. BARDGETT

3.1	Summary	53
3.2	Introduction	54
3.3	Mechanistic Bases of Invertebrate Herbivore Effects	54
3.3.1	Immediate Effects on Resource Quantity	56
3.3.2	Longer-Term Effects on Resource Quantity	56
3.3.3	Effects of Changed Litter Quality	57
3.3.4	Return of Invertebrate Waste Products	58
3.3.5	Effects of Changes in Vegetation Composition	59
3.3.6	Feedbacks and Aboveground Consequences	61
3.4	Significance of Invertebrate Herbivore Outbreaks	61
3.5	Multiple Species Herbivore Communities	62
3.6	Comparisons of Ecosystems	64
3.7	Conclusions	65
	References	66

4 **Biotic Interactions in the Rhizosphere:
Effects on Plant Growth and Herbivore Development** 71

M. BONKOWSKI and S. SCHEU

4.1	Summary	71
4.2	The Rhizosphere – Interface of Intense Microbial and Faunal Interactions	72

Contents	IX
4.2.1 Plants as Drivers of Rhizosphere Interactions	73
4.3 Belowground Interactions and the Herbivore System	74
4.3.1 Effects of Mycorrhiza and Rhizobacteria on Aboveground Herbivores	76
4.3.2 Interactions with the Micro-Decomposer Food Web	77
4.3.2.1 The Bacterial Loop and Herbivore Performance	78
4.3.2.2 The Fungal Food Chain and Herbivore Performance	79
4.3.2.3 Ecosystem Engineers and Herbivore Performance	81
4.4 Top-Down Effects by Subsidizing Generalist Predators	83
References	85
5 Belowground Herbivores and Ecosystem Processes	93
G.J. MASTERS	
5.1 Summary	93
5.2 Introduction	94
5.3 Experimenting with Belowground Insect Herbivores	94
5.4 Belowground Herbivory and Plant Productivity: Allocation and Biomass	97
5.5 Implications of Belowground Herbivory for Nutrient Cycling	101
5.6 Implications of Belowground Herbivory for Multitrophic Interactions	104
5.7 Conclusion	109
References	109
Section III Plant-Insect Interactions and Ecosystem Processes	
6 Bottom-Up Effects and Feedbacks in Simple and Diverse Experimental Grassland Communities	115
J. JOSHI, S.J. OTWAY, J. KORICHEVA, A.B. PFISTERER, J. ALPHEI, B.A. ROY, M. SCHERER-LORENZEN, B. SCHMID, E. SPEHN and A. HECTOR	
6.1 Summary	115
6.2 Introduction	116
6.3 Effects of Plant Diversity on Herbivorous Insects Feeding Above Ground	117

6.3.1	Hypotheses Predicting the Response of Herbivores to Higher Plant Diversity	117
6.3.2	Responses of Specialist and Generalist Herbivores in Plant Diversity Experiments	119
6.3.3	Concomitant Responses of Natural Enemies of Herbivores .	123
6.3.4	Insect Herbivores as Drivers of Ecosystem Processes	124
6.4	Effects of Plant Diversity on Pathogens	125
6.5	Belowground Food Web	126
6.5.1	Plant Biomass and Microbial Response	126
6.5.2	Soil Animals that Feed on Microbes	128
6.6	Conclusions	129
	References	130
7	The Potential of Phytophagous Insects in Restoring Invaded Ecosystems: Examples from Biological Weed Control	135
	H. ZWÖLFER and H. ZIMMERMANN	
7.1	Summary	135
7.2	Introduction	136
7.3	Success Rates and Successes in Biological Weed Control . .	137
7.4	Weed Characteristics and Positive Traits of Insects in Biological Control	138
7.4.1	Weed Species	139
7.4.2	Insect Species	139
7.5	Three Examples of Successful Weed Control	140
7.5.1	<i>Rhinocyllus conicus</i> on <i>Carduus nutans</i>	140
7.5.2	Interactions Between Three Weevil Species in the Biocontrol of the Invader <i>Sesbania punicea</i> in South Africa	143
7.5.2.1	The Seed-Destroying Agents: <i>Trichapion lativentre</i> and <i>Rhyssomatus marginatus</i>	144
7.5.2.2	The Stem-Borer: <i>Neodiplogrammus quadriplagiatus</i>	145
7.5.3	Aquatic Weeds	146
7.6	Discussion and Conclusions	147
	References	150
8	Plant-Insect-Pathogen Interactions on Local and Regional Scales	155
	A. KRUESS, S. EBER, S. KLUTH and T. TSCHARNTKE	
8.1	Summary	155
8.2	Introduction	156

8.3	Biological Weed Control, Interactions and Ecosystem Processes	157
8.3.1	Classical Biological Control	157
8.3.2	Plant–Pathogen–Herbivore Interactions	158
8.4	Creeping Thistle, Insects, Pathogens and Processes	160
8.4.1	The Creeping Thistle (<i>Cirsium arvense</i>)	160
8.4.2	Interactions Between Pathogens and Insect Vectors on a Local Scale	161
8.4.3	Regional Dynamics of <i>Cirsium arvense</i> and an Associated Herbivore	163
8.4.4	The Influence of Landscape Context at Different Spatial Scales	165
8.5	Conclusions and Future Outlook	168
	References	169
9	Food Web Interactions and Ecosystem Processes	175
	A. JANSSEN and M.W. SABELIS	
9.1	Summary	175
9.2	Introduction	175
9.3	Interactions Among Entire Trophic Levels	178
9.4	Effects of Diversity Within Trophic Levels	179
9.4.1	Apparent Competition	180
9.4.2	Omnivory	180
9.4.3	Intraguild Predation	181
9.4.4	Plant-Mediated Indirect Interactions Between Herbivores .	181
9.4.5	Indirect Plant Defences	182
9.4.6	Interactions Among Plants	183
9.4.7	Behavioural Effects	184
9.5	Conclusions and Perspectives	184
	References	186
10	A General Rule for Predicting When Insects Will Have Strong Top-Down Effects on Plant Communities: On the Relationship Between Insect Outbreaks and Host Concentration	193
	W.P. CARSON, J. PATRICK CRONIN and Z.T. LONG	
10.1	Summary	193
10.2	Introduction	193
10.3	The Significance of Insect Outbreaks	194

10.3.1	Insect Outbreaks Are Common in Numerous Community-Types Worldwide	195
10.3.2	Insect Outbreaks Are More Common and More Devastating per Host in Large, Dense and Continuous Host Stands	199
10.3.3	Native Outbreaking Insects Function as Keystone Species by Reducing the Abundance of the Dominant Species and Increasing Diversity	200
10.3.4	Insect Outbreaks Are Common Relative to Host Life Span Yet May Often Go Unnoticed	201
10.3.5	Chrysomelid Beetles and Lepidoptera Seem to be Responsible for the Majority of Outbreaks	201
10.4	The Host Concentration Model May Predict Insect Impact on Plant Communities at Multiple Spatial Scales Better Than Resource Supply Theory	202
10.4.1	Resource Supply Theory	202
10.4.2	The Host Concentration Model (HCM)	203
10.4.3	Distinguishing Between the Two Models	204
10.5	Relationship to Other Related Processes Proposed to Promote Diversity	204
10.5.1	Does Pathogen Impact Increase with Host Concentration? .	205
	References	205
11	The Ecology Driving Nutrient Fluxes in Forests	213
	B. STADLER, E. MÜHLENBERG and B. MICHALZIK	
11.1	Summary	213
11.2	Introduction	214
11.3	Life Histories of Canopy Insects	215
11.3.1	Aphids	215
11.3.2	Scale Insects	215
11.3.3	Lepidopterous Larvae	216
11.4	Population Ecological Background of Nutrient Fluxes . . .	217
11.4.1	Sites and Experimental Setup	219
11.4.2	Results	220
11.5	Trophic Effects and Organic Pathways	224
11.6	Herbivore-Mediated Changes in Quality and Quantity of Nutrient Fluxes	226
11.7	Synthesis and Conclusions	230
11.7.1	Understanding the Temporal Dynamics of Energy and Nutrient Fluxes	230
11.7.2	Understanding the Spatial Variability in Fluxes	231

Contents	XIII
11.7.3 Understanding the Mechanics that Regulate Fluxes	232
11.7.4 Generating Testable Hypotheses	233
References	235

Section IV Methods: Reducing, Enhancing and Simulating Insect Herbivory

12 Simulating Herbivory: Problems and Possibilities	243
J. HJÄLTÉN	
12.1 Summary	243
12.2 Introduction to the Problem	244
12.3 Advantages of Simulated Herbivory	245
12.4 Disadvantages of Simulated Herbivory	247
12.4.1 Simple Biotic Interactions	247
12.4.2 Complex Biotic Interactions	249
12.4.3 Basic Ecosystem Processes	250
12.5 Conclusions and Suggestions for the Future	251
References	253
13 The Use and Usefulness of Artificial Herbivory in Plant-Herbivore Studies	257
K. LEHTILÄ and E. BOALT	
13.1 Summary	257
13.2 Introduction	258
13.3 Material and Methods	258
13.4 Commonness of Differences Between Natural and Artificial Herbivory	260
13.5 Strength of the Effect of Natural and Artificial Damage . . .	266
13.6 Responses of Different Types of Response Traits to Artificial and Natural Damage	267
13.7 Simulations of Mammalian and Invertebrate Herbivory . .	269
13.8 Attempts of Exact Simulation	270
13.9 Conclusions	271
References	273

14	From Mesocosms to the Field: The Role and Value of Cage Experiments in Understanding Top-Down Effects in Ecosystems	277
	O.J. SCHMITZ	
14.1	Summary	277
14.2	Introduction	278
14.3	Research Approach	281
14.4	<i>In-Ecosystem Investigation Using Enclosure Experiments .</i>	282
14.4.1	Natural History: Knowing the Players in the System	282
14.4.2	Enclosure Cages: Design and Biophysical Properties	285
14.4.3	Considerations for the Design of Cage Experiments	288
14.4.3.1	Artificial Complements of Populations or Communities in Enclosure Cages Are Not Realistic	288
14.4.3.2	Experimental Outcome Could Be an Artifact of the Venue .	288
14.4.3.3	Enclosures Unrealistically Constrain Movement of Species .	289
14.4.3.4	Time Scale of Enclosure Experiments Exclude or Distort Important Features of Communities and Ecosystems	290
14.4.4	Mechanistic Insights from Enclosure Cage Experiments . .	290
14.4.4	Identifying the Potential for Top-Down Control	291
14.4.5	<i>Of-Ecosystem Studies: Testing the Reliability</i> of Mechanistic Insights from Cage Experiments	297
14.4.5.1	Direct and Indirect Effects of Top Predators	299
14.4.5.2	Top Predator Effects on Plant Diversity and Productivity .	300
	References	300
15	Reducing Herbivory Using Insecticides	303
	E. SIEMANN, W.P. CARSON, W.E. ROGERS and W.W. WEISSE	
15.1	Summary	303
15.2	Basic Concepts	303
15.3	Using Insecticides to Infer the Role of Herbivores	304
15.4	Ghost of Herbivory Past	307
15.5	Artifacts of Method May Masquerade as Release from Herbivory	308
15.5.1	What Types of Artifacts Are a Concern?	308
15.5.2	Overview of Published Studies	309
15.5.3	Quantification of Herbivore Damage	310
15.5.4	Phytotoxic Effects	311
15.5.5	Insecticides May Be Toxic to Several Groups of Insects .	313
15.5.6	Effects of Insecticides on Non-Arthropods	314
15.5.7	Effects of Insecticides on Soil Organisms	314

Contents	XV
15.5.8 Nutrient Inputs May Facilitate Plant Growth	315
15.5.9 Insect-Vectored Diseases	317
15.5.10 Community-Level Artifacts	318
15.6 Are There Better Types of Insecticides?	318
15.7 Conclusions	319
Appendix: Results of Surveyed Studies	320
References	324
16 The Role of Herbivores in Exotic Plant Invasions: Insights Using a Combination of Methods to Enhance or Reduce Herbivory	329
W.E. ROGERS and E. SIEMANN	
16.1 Summary	329
16.2 Introduction	329
16.3 The Role of Herbivores in Exotic Plant Invasions	330
16.4 Focal Plant Species	331
16.5 Experimental Methods for Assessing Herbivory Effects	331
16.5.1 Common Garden/Reciprocal Transplant Studies	332
16.5.2 Reducing Herbivory on Target Plants	
Using Insecticide Sprays	336
16.5.3 Reducing Herbivory on Community Assemblages	
Using Insecticide Sprays	337
16.5.4 Factorial Manipulations of Herbivory, Resources and Competition	338
16.5.5 Simulating Herbivory Via Mechanical Leaf Damage	339
16.5.6 Simulating Herbivory Via Mechanical Root Damage	341
16.5.7 Simulating Herbivory Using Herbicide Sprays	342
16.5.8 Assessing Herbivore Damage Using Exclosures and Enclosures	344
16.6 Implications and Potential Significance	347
References	349
17 Herbivore-Specific Transcriptional Responses and Their Research Potential for Ecosystem Studies	357
C. VOELCKEL and I.T. BALDWIN	
17.1 Summary	357
17.2 The Subtle Effects of Insects on Ecosystem Function	357
17.3 Transcriptional Regulation of Plant Responses	358
17.4 Insect-Induced Transcriptional Changes	362

17.5	How a Molecular Understanding of Plant–Insect Interactions Can Help Elucidate Ecosystem Function	371
References	375

Section V Synthesis

18	Testing the Role of Insects in Ecosystem Functioning	383
	E. SIEMANN and W.W. WEISSE	
18.1	Summary	383
18.2	Introduction	384
18.3	Simple Models of Niche Space	385
18.3.1	Reduced Vigour Model	385
18.3.2	Reduced Range of Tolerance Model	387
18.3.3	Specialist Herbivores	388
18.4	Effects of Herbivores in Resource Competition Models	389
18.4.1	Specialist Herbivores in Resource Competition Models	391
18.4.2	Generalist Herbivores in Resource Competition Models	395
18.5	Differential Impacts on Plants with Different Traits	396
18.6	Conclusions from the Modelling Work	396
18.7	Suggestions for Future Studies	397
18.7.1	Exploring Below- and Aboveground Interactions in More Detail	397
18.7.2	Measuring Herbivory Effects at Nominal Levels as Well as in Outbreak Situations	398
18.7.3	Quantifying the Effects of Plant Resource Allocation Under Herbivory for Ecosystem Functioning	399
18.7.4	Combining Various Methodologies to Achieve an Understanding of Insect Effects on Ecosystem Function .	399
References	400
Subject Index	403
Taxonomic Index	409