Evaluating Indirect Ecological Effects of Biological Control

Edited by
E. Wajnberg,
J.K. Scott and
P.C. Quimby

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Contents

Contributors xi

Preface xv

1 Indirect Ecological Effects in Biological Control: the Challenge and the Opportunity 1
J.K. Waage

Introduction 1
What will happen to biological control in this century? 2
Efficacy and safety of biological control: a historical perspective 6
Recent developments in biological control 7
The role of ecology 9
Conclusion 10
References 11

2 Indirect Interactions, Community Modules and Biological Control: a Theoretical Perspective 13
R.D. Holt and M.E. Hochberg

Introduction 14
Classical biological control is deliberate 'community assembly' 14
One approach to complexity: community modules 16
Shared predation: identifying extinction risks for non-target prey 18
Disparate impacts of shared predation 19

Simple messages from theory 21
Message I 21
Message II 23
Message III 24
Indirect interactions influence transient risks during agent establishment 27
Landscape-scale indirect effects: the importance of community openness 28
Transient dynamics in shifting landscapes 30
Indirect interactions and evolution 31
Conclusions 31
References 34

3 Research Needs Concerning Non-target Impacts of Biological Control Introductions 39
K.R. Hopper

Introduction 39
Internet workshop on ‘Research needs for assessing and reducing non-target impacts of biological control introductions’ 40
What sorts of non-target impacts should concern us? 40
Host range evaluation 41
Predicting impacts of biological control introductions versus other management options 42
Retrospective studies to assess impacts 43
Montpellier workshop on ‘Evaluating indirect ecological effects of biological control’ 44
Session I: identification of major research questions 45
Session II: approaches to answering selected questions 47
Conclusions 54
References 55

4 Food Webs, Risks of Alien Enemies and Reform of Biological Control 57
D.R. Strong and R.W. Pemberton

Introduction 58
Biological control in conservation 58
Food webs, direct and indirect interactions 59
Differences between natural and cultivated systems 63
Risks of biological control 63
Weed biological control 65
Insect biological control 66
Parasitoids and general predators 66
Ladybird beetles 68
The campaign against Russian wheat aphid 69

Reform of biological control 70
References 74

5 Evaluation of Non-target Effects of Pathogens Used for Management of Arthropods 81
M.S. Goettel and A.E. Hajek

Introduction 82
Types of control 83
  Classical biological control 83
  Inundative augmentative releases 86
Non-target effects of pest control using entomopathogens 87
  Classical biological control 88
  Inundative augmentative releases 91
  A special case: genetically engineered pathogens 92
Methods for evaluating non-target effects 92
Conclusions 94
References 94

6 Insect Biological Control and Non-target Effects: a European Perspective 99
L.D. Lynch, H.M.T. Hokkanen, D. Babendreier, F. Bigler, G. Burgio, Z.-H. Gao, S. Kuske, A. Loomans, I. Menzler-Hokkanen, M.B. Thomas, G. Tommasini, J.K. Waage, J.C. van Lenteren and Q.-Q. Zeng

Introduction: the ERBIC project 100
A retrospective analysis of published and unpublished data 102
  Methods 102
  Results 104
  Database conclusions 112
Case studies in European biological control 113
  Case 1: exotic specialist parasitoids 114
  Case 2: exotic generalist parasitoids 116
  Case 3: generalist exotic predators 118
  Case 4: fungi and nematodes as bioinsecticides 120
Mathematical modelling and ecological theory 121
Overview 122
References 123

7 Biological Control in Africa and its Possible Effects on Biodiversity 127
P. Neuenschwander and R. Markham

Introduction 128
Case studies 131
  Cassava mealybug 131

Mango mealybug 133
Spiralling whitefly 134
Cassava green mite 135
Lepidopterous stemborers 136
Cowpea thrips 137
Larger grainborer 138
Water hyacinth 140
Fungal pathogens against grasshoppers 140
Discussion 141
References 144

8 *Rhinocyllus conicus*: Initial Evaluation and Subsequent Ecological Impacts in North America 147
A. Gassmann and S.M. Louda

Introduction 148
Natural history of *Rhinocyllus* 150
Pre-release studies in Europe (1961–1968) 151
Early field studies 152
Early laboratory studies of host acceptance, preference and performance 153
Early post-release studies (1969–1985) 156
Field studies in Europe 156
Laboratory and greenhouse studies of preference and performance in North America 158
Garden plot and field studies in North America 158
Recent studies of *Rhinocyllus* (1986–1999) 161
Variation in phenology 161
Phenotypic and genetic variation in host use 161
Non-target feeding on *Cirsium* species in North America 163
Thistle–insect interactions in prairies of the upper Great Plains 164
Altered ecological interactions in the new environment? 167
Discussion 169
Host specificity: feeding acceptance, oviposition and larval performance 170
Host specificity: larval survival and performance 172
Prediction of quantitative ecological effects 173
Conclusions 174
References 176

9 Risk Analysis and Weed Biological Control 185
W.M. Lonsdale, D.T. Briese and J.M. Cullen

Introduction 186
Risk analysis and biological control: some definitions 187

Comparative risk analysis (CRA) 188
Risk assessment 188
  The NAS model 188
  Ecological models of risk assessment 189
  Difficulties of prediction 190
  Prediction tools 193
  Risk scenarios 196
Risk management 200
Risk communication 201
  Background 201
  Release application procedures in different countries 201
  Precautionary principle 202
  Good and bad risk communication 203
Monitoring 203
Synthesis 204
References 205

10 Incorporating Biological Control into Ecologically Based Weed Management 211
R.L. Sheley and M.J. Rinella

Introduction 211
Management objectives 212
Need for predictive capability 212
Mechanisms and processes directing plant community dynamics 213
Incorporating biological control into ecologically based weed management 215
Modelling and predicting weed management's influence on community dynamics 215
  Successional weed management 215
  Designed disturbance 216
  Controlled colonization 217
  Controlled species performance 218
  Examples 219
  Life-history models 221
Assessing the indirect impacts of biological controls using community dynamics models 225
References 225

11 The Scope and Value of Extensive Ecological Studies in the Broom Biological Control Programme 229
S.V. Fowler, J. Memmott, Q.E. Paynter, A.W. Sheppard and P. Syrett

Introduction 230
Scotch broom, *Cytisus scoparius*, as a target for biological control 231

- Ecological studies undertaken on broom in its native range in Europe and elsewhere 232
- The value of ecological studies in predicting the success and safety of biological control of broom 239
  - Predicting the impact of agents for the biological control of broom 239
  - Predicting side effects after the introduction of a biological control agent against broom 240
- Conclusion 243
- References 245

Index 249

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Preface

Within the last few decades, classical biological control – the introduction of exotic natural enemies to reduce the abundance of exotic pests or weeds – has been practised more and more frequently worldwide as successes accumulate and as new exotic pest or weed problems follow trade liberalization. The efficacy of the method lies in the ability of the introduced natural enemies to reproduce and spread – and thus to persist – in the environment. Accordingly, biological control is now considered by many to be a real ecological process and, as such, the associated risk through both direct and indirect effects on non-target species has to be considered, quantified and avoided.

Biological control programmes have been developed and used for almost a century and, compared with chemical pesticide alternatives, studies of their associated potential environmental risks have often been neglected. Only recently have the ecological non-target effects of biological control finally been recognized and studied. This has been fostered by growing concerns about the need to preserve biodiversity and natural ecosystems. This is the reason why the International Organization for Biological Control of Noxious Animals and Plants (IOBC) decided to organize the first international symposium on this subject at Montpellier, France, 17–20 October, 1999. This symposium, entitled 'Indirect Ecological Effects in Biological Control', was also sponsored by the Complexe International de Lutte Biologique-Agropolis (CILBA) and AGROPOLIS. This book is a collation of key papers presented at this symposium.

The different topics are arranged into 11 chapters and were chosen in order to present both general considerations and detailed case studies of non-target effects in classical and augmentative use of arthropods and microbes for biological control of pest insects and alien weeds. All papers and references to genetically modified organisms were consciously limited in order to focus the discussion on natural systems of biological control. The editors of the book were especially interested in papers which might provide previously unrecognized or unappreciated methods for measuring or determining non-target effects of biological control agents. As a result, the authors include theoretical or classical ecologists, but also practitioners of biological control, who are considered by many to be applied ecologists.

After a general introduction (Chapter 1), a theoretical approach to the analysis of ecological non-target effects of biological control is developed (Chapter 2). Then, the most important questions that need to be addressed by the scientific communities are listed in the following chapter. These questions were raised both during the symposium itself and during a workshop organized on the Internet during 9 months in 1999. Then, based on an analysis of the different risks of biological control, Chapter 4 develops a discussion of the potential reform that might be proposed in order to reduce the ecological non-target effects to their minimum.

It is not possible to discuss the risks of biological control without an accurate survey of the known problems that have surfaced after the release of biological control agents. Chapter 5 analyses the potential non-target effects in the use of pathogens (i.e. microorganisms) to control insect pests, while Chapter 6, based on a European research programme, presents a detailed analysis of the relevant information that can be found in databases gathering all sorts of non-target effects observed after biological control programmes against insect pests worldwide. Then, Chapter 7 gives a detailed analysis of different case studies related to biological control in Africa, and their potential risks to biodiversity.

One of the best-known examples of negative direct and indirect ecological effects of the use of a biological control agent is the release of the flowerhead weevil, *Rhinocyllus conicus* Fröl., in North America for the biological control of true thistles, especially in the genus *Carduus.* Chapter 8 gives a detailed summary of this particular case and discusses why and how such non-target impacts could have been avoided. Concerning weed biological control, the following three chapters (9, 10 and 11) then discuss, respectively: risk analysis and assessment; ecologically based plant community dynamics; and predicting the impact of agents in the particular case of the broom biological control programme.

The chapters included here were selected to provide a scientific basis for needed reform and improvement in the practice of biological control worldwide. The editors are deeply grateful to the authors who have contributed so magnificently to that goal, and also to several anonymous reviewers who greatly improved the final quality of the book. Dr Jeff K. Waage deserves a special 'thank you'. Without his continuous encouragement and support, this book would not exist.

Eric Wajnberg
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1

Indirect Ecological Effects in Biological Control: the Challenge and the Opportunity

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Abstract

The spread of integrated pest management (IPM) practices and concern for the environmental impact of alien invasive species will increase demand for biological control in the next century. Meeting the demands of a broader stakeholder community will require further development and harmonization of international protocols, with greater attention to non-target, ecological effects. Ecological theory and research has a key role to play in delivering tools to evaluate these effects, thereby improving efficacy and safety of biological control.

Introduction

Biological control has become today a key component of crop protection worldwide. Concern about reliance on chemical pesticides has led to the development of integrated pest management (IPM), which depends on both the conservation of local natural enemies and their mass release as alternatives to chemicals. Classical biological control, the introduction of exotic biological control agents to permanently suppress exotic pests, is practised ever more widely as successes accumulate, and as new exotic pest problems follow trade liberalization. The capacity of introduced natural enemies to persist in the environment, to reproduce there and to spread gives biological control its unique advantage as a pest control method. It also binds the practice of biological control to the science of ecology,

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through which it can be understood, and it identifies an element of risk through indirect effects of new natural enemy populations on local communities and non-target species.

While there has been much discussion of the risks of biological control in the past few years, there has been little attention given as yet to the development of practical methods for better evaluating non-target effects as a basis for risk assessment. This book addresses this challenge. It follows an international symposium organized in October 1999 by the International Organization for Biological Control of Noxious Animals and Plants (IOBC) in Montpellier, France, and the 'Complexe International de Lutte Biologique Agropolis' (CILBA) at Agropolis International.

IOBC was established in 1957 to promote biological control and its application, and today comprises over 2000 scientists around the world, collaborating in global and regional working groups. IOBC recognizes that, as biological control attracts interest and investment from ever broader sections of society, it is also held more accountable in terms of its efficacy and safety. Biological control scientists must provide these stakeholders with sound methods for their evaluation in order to ensure its progress in the coming century.

The symposium was designed to bring together ecologists and biological control specialists from around the world to examine the known and possible ecological effects of introducing biological control agents on species other than the target pest and on the communities and ecosystems in which they live. Many of the presentations focused on new methods for evaluating non-target effects. A set of abstracts of all presentations has already been published by IOBC (1999). The chapters in this volume are drawn largely from keynote presentations at this symposium, while Chapter 3 summarizes the results of a workshop to identify priorities for future studies.

In this introductory chapter, I will examine the context in which methods for evaluating non-target effects of biological control need to be developed. I will consider likely future trends in biological control introductions. Then, I will show how the history of safety testing in biological control has left us with particular needs today. Finally, I will suggest why ecological theory and research have a particular value in developing the methodology that we need.

What will happen to biological control in this century?

Pest control is today emerging slowly from an era of dependence on chemical pesticides under a new paradigm of IPM, in which biological control figures importantly because of its potential to be safe to humans, environmentally friendly and self-sustaining. An increasing number of agricultural systems and countries have experienced encouraging successes with classical biological control of alien pests and the use of biological products in IPM systems. Even organic production systems, while still commanding a very small proportion of developed country markets, are having an influence far greater than their market share on sensitizing the public to the issues surrounding biological pest control.

While a chemically oriented approach to research and extension in pest control still persists in most countries, governments are acting more and more to remove factors which inhibit biological control (e.g. pesticide subsidies, regulatory barriers) and to provide incentives for biologically based technologies. Overall, the demand and opportunity for biological control is greater than ever and it would appear that, in contrast to a few years ago, its potential for growth is no longer limited by competitiveness with chemicals, but by its inherent applicability to particular pest problems.

The growth of two approaches to biological control interests us particularly in this book: augmentation of natural enemies, usually as commercial products, and introduction of natural enemies as 'classical' agents, because both of these methods may involve release of species into new environments. Despite decades of development, augmentative biological control (including the development of mass-produced pathogens of pests as commercial biopesticides) is not widely used (Lisansky, 1997). Commercial biological control products have faced stiff competition from chemical products and only a few have developed a substantial market. Preparations of *Bacillus thuringiensis* (Bt) are responsible for the great majority of commercial sales of microbial agents, while macrobial agents (predators and parasitoids) have smaller but secure markets in the protected crop sector in temperate countries and in a few tropical crops like sugarcane. Today, a substantial number of augmented biological control agents are alien to the habitats where they are released. The decision to introduce an alien biological control agent, in preference to commercializing a local species, often has less to do with their relative efficacy and safety than with the availability of an existing product, set against the cost of developing a new one. In continents like Europe, most introductions of alien biological control agents today are for this commercial sector, rather than for classical biological control. Many commercial biological control agents, particularly microbials, are not expected to establish or to spread, but the possibility exists. The introduction of these products into countries involves registration procedures for pest control products, which are usually different from procedures for introduction of new species, e.g. through quarantine.

Augmentative biological control is growing and this trend will probably continue or even accelerate due to new demand from farmers who are moving away from chemical pesticide use. Driving factors here will be the future withdrawal of particular chemical products, e.g. organochlorine and organophosphate insecticides, which will create new market niches for biological products, and the spread of certified production in IPM and organic systems, which will require more non-chemical approaches. Recent evaluations of augmentative control suggest that its future growth will also depend on moving away from traditional product models that fashion biological products as little more than chemical pesticide replacements (Waage, 1997). Specific trends identified include: (i) greater exploitation of properties which make biological products superior to chemicals, namely their self-renewing and self-spreading powers; and (ii) greater reliance on local production and distribution systems for high-quality products, which addresses problems of product specificity, storage and farmer education. The first factor would tend to increase the need for understanding non-target effects, as it will encourage persistence of released organisms; while the latter may put strong emphasis on the development of local species and strains, which would reduce risks of non-target effects. Of course, even local biological control agents released into habitats in unusually high numbers may have non-target effects that would not occur at normal population levels.

Classical biological control of alien pests developed during the 20th century largely as a public sector activity, because its benefits cannot easily be restricted and because it has very high initial costs of research and safety testing. Federal and state agriculture departments commonly mount classical biological control programmes, and some have a long tradition in this area. However, it is fair to say that, until one or two decades ago, most governments turned to classical biological control only as a last resort, after chemical and physical control methods against new pests had failed. Today, due to recent successes in classical biological control and concern about extensive use of pesticides against a new alien pest, this situation has changed.

Analyses of trends over the last century in the introduction of classical biological control of invertebrates and weeds show steady growth (Greathead and Greathead, 1992). Today, over 6000 introductions of agents for control of alien invertebrate pests have been made and about 1000 introductions for control of alien weeds (Julien and Griffiths, 1998). There are a number of reasons to believe that this growth will continue. Firstly, alien pest, weed and disease problems in agriculture are increasing due to an increased volume of international trade and to the opening of new trade routes. For instance, the opening of trade between temperate Asia, including the formerly isolated Soviet Union and China, and the rest of the world has quickly led to the introduction of serious alien forestry pests in all of these temperate regions.

Growing North–South trade and South–South trade in high-value horticulture and the establishment of new, tropical production centres have been responsible for the rapid spread around the world of such vegetable pests as whiteflies (e.g. *Bemisia argentifolia*) and leafminers (*Liriomyza* spp.). Secondly, governments in developing countries, and the development agencies which support their need for international assistance, see alien pest species today as threats not just to national commerce but to sustainable development itself. In recent decades, serious alien pests of staple cereal production have spread around the developing world, including rice water weevil (*Lissorhoptrus oryzophilus*), corn rootworm (*Diabrotica virgifera virgifera*), golden apple snail (*Pomacea canicularis*), itchgrass (*Rottboellia cochinchinensis*) and maize borer (*Chilo partellus*). At the same time, invasive alien weeds have emerged as major constraints to reforestation, water management and recovery of degraded lands in developing countries, all high priorities for international development. For these affected developing countries, where farmers have very few resources for pest control, classical biological control of these alien arthropod and weed pests may be the only economical management option (see Neuenschwander and Markham, Chapter 7, this volume). Development assistance agencies have been very active in supporting classical biological control as a sustainable solution for resource-poor farmers affected by alien pests.

Finally, beyond agriculture, the global environmental community has now recognized that alien invasive species pose particular threats to the conservation of biological diversity. The 1994 Convention on Biological Diversity requires countries to 'Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species' (Article 8h). A meeting of national delegations and environmental experts in 1996 (Sandlund *et al.*, 1996) concluded that alien invasive species were the second greatest threat to biodiversity conservation next to habitat destruction. The scale and ecological sensitivity of these conservation problems makes biological control, with its potential specificity and self-spreading nature, particularly attractive as a management tool. Indeed, many of the most serious environmental invaders are weed species that have already been the target of biological control research in an agricultural context. With the development of new initiatives like the Global Invasive Species Programme (Mooney, 1999), classical biological control has become recognized as a valuable potential technology in the toolkit of alien invasive species management.

In summary, augmentative and classical biological control are likely to grow rapidly over the next decade, involving both the public and private sectors, and involving countries and communities with very different levels of experience in this technology. While classical biological control has a public sector base, and hence an internal regulatory framework, export and import of alien biological control agents for commercial purposes will attract greater application of formal registration and regulatory systems, including safety testing. At the same time, new stakeholder groups for classical biological control, such as development agencies, environment departments and conservationists, will have greater concerns about environmental safety and non-target effects than traditional stakeholders in the agricultural sector. How are our systems for measuring non-target effects, and thereby ensuring the efficacy and safety of introduced biological control agents, prepared for this growth in both augmentative and classical biological control?

Efficacy and safety of biological control: a historical perspective

Many people who do not know much about biological control *do* know about the disastrous attempts in the 18th and 19th centuries to use general predators such as birds and mongooses for control of animal pests on tropical islands. These predators, once established, included in their diet more vulnerable, indigenous species, driving some to extinction. While biological control has moved on from these faltering first steps, these stories provide a continuing warning that biological control holds risks for non-target species, and that it can be both ineffective and unsafe. This warning was sadly refreshed during the 20th century by a few repetitions of vertebrate predator introductions, such as the cane toad, into some tropical and subtropical countries.

Biological control only attracted serious scientific interest once it began to demonstrate high levels of both efficacy and safety. Promising results emerged from projects in the late 19th century and early 20th century with the use of insect control agents, first for control of alien insect pests, and then for control of alien invasive weeds. Landmark studies were the introduction of the ladybird, *Rodolia cardinalis*, against the alien cottony cushion scale in California in 1888, and the introduction of the moth, *Cactoblastis cactorum*, and other natural enemies, against prickly pear cactus in Australia in the 1920s (Debach, 1974). In retrospect, we know that the key to success in these projects was the use of organisms that were relatively specific to the target alien pest.

In contrast with vertebrate predators, many insect natural enemies show a high degree of specificity to particular kinds of prey or hosts. Specificity conferred a degree of safety in these now ‘classical’ biological control programmes by ensuring that agents did not attack a wide range of unrelated non-target species in their new environment. It was some years later that ecological studies would show precisely how specificity enhanced efficacy as well, by ensuring that the agent tracked effectively the density and distribution of the pest population, thereby causing both considerable suppression and a degree of regulation through density dependent mortality of the pest (Hassell, 1978).

The importance of specificity to both the safety and the efficacy of biological control introductions gradually made it an important criterion in the selection of biological control agents. For both weed and insect targets, valuable information on host specificity could be obtained from information on the taxonomic associations of natural enemy and host groups, which are often clearly evolutionary, even co-evolutionary, in origin. Many biological control agents, including insects and plant pathogens, belonged to groups which appeared to be restricted to certain genera or families of pests or weeds, and some appeared to be even more specific.

A tradition of safety studies to ensure specificity of biological control agents did not develop overnight, and it happened more rapidly with some kinds of biological control than with others. Specificity testing in weed biological control developed most rapidly, simply because of the more obvious threat which introduced plant-feeding insects posed to crops, relative to the predators or parasitoids of insect pests. It included both tests on crop plants and, later, the inclusion of plant species related to the target weed, to establish experimentally the taxonomic limits of host range in potential control agents. These tests have led today to a set of procedures which are widely agreed between weed biological control specialists, but still frequently re-examined and debated (Withers *et al.*, 1999; see also Lonsdale *et al.*, Chapter 9, this volume; and Sheley and Rinella, Chapter 10, this volume). For biological control of arthropods, specificity testing has lagged behind that for weeds, because concern for non-target effects on invertebrates has not been so great. Only recently have local insects of conservation or agricultural value (i.e. natural enemies of pests) been added for safety studies to the traditionally short list of bees and silkworms. One of the significant outcomes of the IOBC symposium of October 1999, however, was the degree of consensus reached between insect and weed biological control specialists on requirements for safety testing in future (see Hopper, Chapter 3, this volume).

Recent developments in biological control

It should be clear from this short history that biological control developed as an agricultural technology, and its procedures for non-target studies and safety testing reflect this strongly. It is not surprising, perhaps, that the safety record of biological control with respect to agricultural production has been extremely good. There are virtually no records of invertebrate and microbial biological control agents introduced through standard safety procedures becoming significant agricultural pests. The few reported instances of impact on non-target crops appear to have been transient demographic or behavioural effects. For instance, lacebugs (*Teleonemia scrupulosa*) released against *Lantana camara* on sesame in Uganda attacked sesame crops at the peak of their populations, but this feeding disappeared as damaged *Lantana* supported lower lacebug populations (Davies and Greathead, 1967). More recently, leaf beetles (*Zygogramma bicolorata*) introduced against *Parthenium hysterophorum* attacked sunflower in India (Jayanth *et al.*, 1993, 1998) during similar population peaks, most likely encouraged by the presence of parthenium pollen on sunflower leaves, which acted as a feeding stimulant. Again, no reproduction of the agent on the crop occurred and the effect appeared to be locally transient.

Overall, the record of biological control over recent decades has given the agricultural sector confidence in existing safety testing procedures. The major concern of this sector has been the formalization and widespread adoption of these procedures. Biological control is increasingly practised by countries and organizations within them with little experience in this technology. In the 1990s, scientists and governments identified a need to formalize procedures for biological control introductions and to harmonize practice across countries. With assistance from specialists from developing and developed countries, and input from FAO, CABI and IOBC, a Code of Conduct for the Import and Release of Exotic Biological Control Agents was produced in 1995 (Greathead, 1997). It describes the responsibilities of all parties involved in biological control introductions, including the preparation of dossiers for candidate agents, which include ‘an analysis of the host specificity of the biological control agent and any potential hazards posed to non-target hosts’. However, as yet, specific guidelines for testing non-target effects have not been prepared.

Subsequently, governments and regional plant protection authorities have taken these guidelines and adapted them to local or regional needs. In Europe, for instance, the European Plant Protection Organization has adapted the Code to address particularly the issues raised by the introduction of biological control agents for research and commercial purposes. Parallel to this international activity has been a great deal of national activity in the development of regulatory systems for biological control introductions. Considering that classical biological control programmes are usually undertaken by the same government agencies as those responsible for the regulation and safety of biological control, opportunities for conflict of interest are substantial, and formal, transparent regulatory procedures do provide important credibility to the process.

In the past decades, however, another substantial challenge has arisen for safety testing in biological control. Conservation ecologists have observed and documented possible effects of introduced biological control agents on non-target species not associated with agricultural systems (Howarth, 1991; Simberloff and Stiling, 1996). Records of these non-target effects were, like most records of past biological control, often sketchy on detail and easy to debate. This debate about the existence and scale of non-target effects against local species in natural ecosystems gave way eventually to a general consensus that, with their historical focus on threats to agricultural systems, past biological control programmes may not have evaluated threats to natural ecosystems to the extent that would be desirable today. Only new research can determine how important these non-target effects on local species and natural ecosystems might be, and how they might be better avoided through safety testing procedures.

The need to address the effect of biological control introductions in natural ecosystems is made more urgent by the growing interest in biological control as a tool in the management of alien invasive species affecting conservation. This new focus requires that traditional approaches to evaluating non-target effects be modified to reflect the needs of a stakeholder community whose principle objective is the conservation of species and ecosystem processes, and not the elimination of a particular pest affecting the productivity of that ecosystem. This community logically puts an understanding of indirect ecological effects of biological control as a high priority.

The role of ecology

It is frequently said that biological control is the application of ecology in pest management. Ecological research has contributed both theory and methodologies, such as life table analysis, to the practice of biological control. By virtue of ecological theory, we understand better the important relationship between the specificity of a control agent, its efficacy and its impact on pest populations. Theory has allowed us to go further and compare properties of biological control agents as they affect success in the field, but it has not given us the strong predictive tools, which it may have promised some decades ago. Because of the nature of biological control programmes, our capacity to predict the outcome of biological control introductions lies today in: (i) the accumulation of experience from previous biological control programmes; (ii) retrospective hypothesis creation and testing using specific, completed programmes; and (iii) the prospective application of broad principles arising from theory in the selection of agents (e.g. for specificity, density dependence, impact on vulnerable life stages of the pest). While this is an imperfect source of predictive power, it is none the less a valuable one, which grows as biological control records accumulate and as we make the commitment today to better pre- and post-release studies in biological control.

Ecological theory has considerable potential to help us to understand and predict indirect ecological effects of biological control. This potential is virtually unrealized because we have concentrated our theoretical attention so far mainly on the impact of an agent on a target, rather than a non-target, species (however, see Holt and Hochberg, Chapter 2, this volume). In theoretical terms, there is little difference, and what we understand about searching efficiency, spatial patterns of mortality, the role of density dependence and the importance of vulnerable and invulnerable life stages applies equally well to the study of target and non-target species. There is already a substantial theoretical experience in biological control with multi-species interactions at different trophic levels. In the 1970s, for instance, ecologists and biological control experts spent considerable energy considering the value of single vs. multi-species introductions of control agents, particularly for insect pest control. Theoretical models revealed considerable potential for competitive displacement of one agent by another, which was borne out in classic studies on scale insects, fruit flies and other biological control systems (Hassell and Waage, 1984). However, the emphasis of the research was more on the biological control outcome than on the composition of the natural enemy community at the end of the interaction. When we look at our competing natural enemies as comprising alien and native species, this body of theory and research takes on new and useful dimensions with respect to non-target testing. Similarly, considerable ecological theory has been directed at the behaviour of generalist vs. specialist natural enemies, and their capacity to suppress and regulate populations (Hassell, 1986). The capacity of generalists to 'switch' between hosts, and its consequences, has been extensively studied and modelled. Once more, the emphasis has been on impact on target pests, not non-targets.

When we set out to develop a theoretical framework for the study of non-target effects in classical biological control of invertebrate pests, two simple, and much researched, theoretical systems hold promise: two-predator, one-prey models, and one-predator, two-prey models (see Holt and Hochberg, Chapter 2, this volume). Most non-target effects causing the greatest concern today fall into one of these categories, e.g. the impact of introduced coccinellids on native species (see Lynch *et al.*, Chapter 6, this volume) and the impact of introduced herbivores on native plants (see Fowler *et al.*, Chapter 11, this volume), respectively. Exploring simple models like these, therefore, might help to identify what factors would be the most important to measure in order to gain an understanding of potential non-target effects in a particular biological control programme. Further, these models might not just help us to understand the endpoint of multi-species interactions, but perhaps more importantly their trajectory, the period of intense population change after introduction, when we might actually be measuring non-target impacts and drawing our conclusions about the safety of a biological control programme. This modelling activity is now linked to a programme of research on different predator–prey and parasite–host systems across Europe, the European Union project on Evaluating Risks of Biological Control (ERBIC) which is described by Lynch *et al.* (Chapter 6, this volume).

Theoretical ecologists and biological control scientists have been looking at and predicting non-target effects for years, but in a very different context from the challenge posed to us today. We have the opportunity now to review and adapt this knowledge to a new purpose, to select that which is valuable and to build on it a new ecological framework for the evaluation of non-target effects, which must underpin any future, practical measures in this area.

Conclusion

This book, and the IOBC symposium organized on the subject, attempt a dialogue between ecologists and biological control experts to develop methods for evaluating indirect ecological effects of biological control. These methods will make a contribution to decision-making about future biological control programmes or introductions. That decision-making process depends on wide consultation with the stakeholder community, not just on the contributions of scientists. Within this process, scientific research has a key role to play in improving efficacy and safety in biological control and in developing tools to evaluate both. In so doing, it will help to support biological control.

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2

Indirect Interactions, Community Modules and Biological Control: a Theoretical Perspective

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Abstract

Indirect interactions are almost inevitable in any multi-species community. Understanding the implications of such interactions is a challenging task, in light of the very large number of ways species can be tied together in complex food webs. One approach to this complexity is to focus on strong interactions among a relatively small number (e.g. 3–6) of species interacting in defined configurations: community modules. In recent years, the discipline of community ecology has developed a substantial body of theory focused on such modules. Modules often clearly describe the basic features of empirical systems, particularly in simplified anthropogenic landscapes, and also help to isolate and characterize key processes driving the dynamics of more complex communities. In this chapter, we draw out a number of insights from ecological studies of modules which we believe are relevant to biological control. We emphasize in particular the module of 'shared predation', where a natural enemy attacks two or more species of prey. Theoretical studies suggest a number of 'rules of thumb', including: (i) the greatest risk to non-targets may occur from control agents that are only moderately effective on the target; (ii) targets with a high reproductive capacity can indirectly endanger non-targets; (iii) there can be transient phases of extinction risk for non-targets during the establishment phase of control agents, particularly for species with high attack rates; (iv) at a landscape scale, mobile agents can endanger the fate of non-targets at sites

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other than the area of control; (v) using specialist natural enemies can pose risks to non-targets, if there are generalist resident predators/parasitoids which can exploit these introduced agents. The theoretical models help to highlight circumstances when these effects should be particularly strong.

Introduction

Recent years have seen a growing chorus of concerns about classical biological control because of the potential harm posed by non-indigenous control species, introduced to control exotic pests but also influencing the lives of other, non-pest species (Simberloff and Stiling, 1996; Williamson, 1996; Hawkins and Marino, 1997; Frank, 1998; Hopper, 1998; Philogène, 1998; Thomas and Willis, 1998; Walter *et al.*, 1998). Our purpose in this chapter is to stand back from the details of particular systems and cost/benefit analyses, so as to provide a perspective from more general theoretical studies in community ecology. We will not dwell on the details of equations, but rather on broad conceptual insights in community ecology which we believe are pertinent to indirect effects of biological control.

Generalizations in ecology are often necessarily cast at a broad scale, but are hardly ever universally true (Lawton, 1999). The laws or rules that we do have are often contingent in form, tailored to particular sets of organisms and given structures of interactions and environments. A broad message emerging from community ecology in recent decades is that indirect interactions among species are pervasive in natural communities (Bender *et al.*, 1984; Polis and Holt, 1992; Menge, 1995, 1997). Such interactions are often quantitatively as important as direct trophic or interference interactions, and can occur even over short time-scales (Menge, 1997). Indirect interactions arise because most species live in a complex web of interactions, and in principle this makes it difficult to predict the response of even well-understood systems to environmental change (Yodzis, 1988). Some ecologists even despair of identifying general patterns (Polis and Strong, 1996). Despite these complexities and difficulties, however, we would argue that the development of management tools to address specific biological control problems can draw useful messages from the basic insights of theoretical studies of indirect interactions. Such studies identify major, repeatable themes which biological control practitioners can incorporate into their conceptual repertoire.

Classical biological control is deliberate ‘community assembly’

The use of non-indigenous species in pest control, and the potential impact of such species on native non-target species, represents an applied analogue of a basic theme in ecology, *assembly dynamics*. Over time, local communities necessarily arise from a historical process of assembly (Holt, 1993; Ricklefs and Schluter, 1993), involving both colonization from larger biogeographical regions and local extinctions. A central theme of community ecology (in some ways, its most basic paradigm (Law and Morton, 1996)) is that local communities (defined at spatio-temporal scales where individuals can potentially interact) are restricted subsets of larger regional pools (Roughgarden and Diamond, 1986). This restriction may arise due to chance, or because species' basic autecological requirements are not met at a particular site, or because of interactions between invaders and residents. In the last case, community structure (i.e. non-randomness in species composition) arises because of patterns in the success or failure of repeated invasion attempts (e.g. exclusion of invaders by competition with or predation from resident species).

Understanding community assembly in general requires one to consider three distinct processes. First, one focuses on the ability of an invading species to increase when rare – *establishment*. If a given species always declines rapidly to extinction whenever it attempts to colonize, it will not become a member of the local community. Second, following establishment, one examines the effects (direct and indirect) of the successfully invading species upon the local community – its *impact*. In some cases, invasions may have little impact. For instance, a commensal specialized to a single species may invade and have very little impact on the resident community, so there is a simple additive increase in local species richness. If, by contrast, a highly effective predator or competitor for local resources invades, a single invasion can unleash a wave of local extinctions, so local species richness declines. Third, in many circumstances one must explicitly consider flows of individuals and resources among spatially distinct communities – *landscape context* (Holt, 1996; Polis *et al.*, 1997). Some species may be present in a local community because of sufficient rates of recurrent immigration (the 'mass effect' of Shmida and Wilson, 1985). This can quantitatively influence local dynamics in a wide variety of ways, for instance by providing alternative prey for resident predators (Huxel and McCann, 1998). Other species may only persist precisely because they can utilize a variety of habitat types (Holt, 1997a). The importance of these effects depends on many different aspects of landscapes (e.g. patch areas and shapes, connectivity) and is an active area of research (Polis *et al.*, 1997).

These three fundamental aspects of community assembly processes – establishment, impact and landscape context – are also basic considerations in evaluating potential indirect effects of introduced biological control agents. We will focus on impact and landscape context, rather than establishment.

One approach to complexity: community modules

In the past few decades, there has been substantial growth in our understanding of the dynamics of single populations (e.g. in the conditions that promote chaos or stability, or in dealing with the intricacies of stage-structured dynamics). The discipline of community ecology is not so well developed. The basic reason for this is that ecological communities are incredibly complex entities. We are all familiar with depictions of food webs articulated at the species level, which resemble a tangled plate of spaghetti (e.g. Winemiller, 1990; Closs *et al.*, 1999); merely compiling the information to construct such webs involves a gargantuan effort, and at the end one is still far from a clear understanding of the dynamics governing the system. We have argued that a useful conceptual way-station between the relative simplicity of single-species dynamics and the almost overwhelming richness of entire communities is the analysis of *community modules* (Holt, 1997b). The basic idea is that there are recurrent structures, involving a small number (e.g. 3–6) of species interacting in a specified pattern, often (although not necessarily) strongly. These modules involve multi-species extensions of basic pairwise interactions (e.g. host–parasitoid dynamics).

Figure 2.1 depicts a smorgasbord of some of the most familiar of these modules, cast so as to be relevant to biological control. There are a number of rationales for focusing on community modules. First, empirical systems may closely match the structure of a module. Subwebs of natural communities with strong interactors and well-defined functional groups often quite naturally fit a particular module (e.g. Evans and England, 1996). Given that biological control agents are deliberately chosen to have a strong interaction with at least one other species – the target species one would like to control – then a modular structure may readily be discerned in many control situations. Second, modules can be viewed as building blocks of full, complex communities. Close analyses of modules permit one to isolate certain key processes which may be general drivers of the dynamics of entire communities. The discipline of community ecology is replete with theoretical and empirical studies of community modules (e.g. May and Hassell, 1988; Holt and Lawton, 1993, 1994; Holt, 1997b). The broad aim of the remainder of this chapter is to relate insights from this body of work in basic ecology to the applied problem of indirect impacts of biological control. We will focus in particular on risks posed by shared predation, which may be the most general situation in biological control where a consideration of indirect interactions is important. Murdoch and Briggs (1996) note that although ecological theory has not historically been all that useful in the practice of biological control, recent theoretical advances in population dynamics do have important messages for practitioners. We suggest that the same is true for theoretical studies of multi-species interactions.

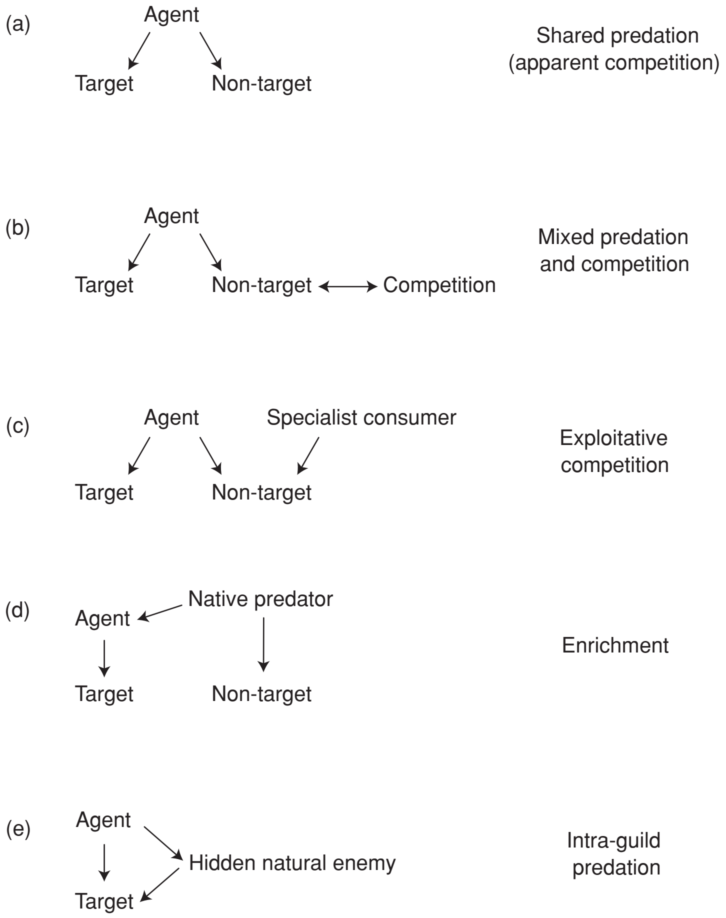

Fig. 2.1. Community modules. The word ‘module’ refers to a specified structure of interactions among a small number of species. A number of modules are likely to describe indirect impacts of biological control. For simplicity, the lines indicate that two species interact (a more detailed food web diagram would have pairs of arrows and signs, describing reciprocal impacts of each species). (a) Shared predation: impacts upon non-targets reflect interactions between agent and target (as in apparent competition). (b) Mixed predation and competition: impacts upon non-targets are aggravated by the presence of competing species. (c) Exploitative competition: the agent exploits a non-target species which is required by another non-target consumer. (d) Enrichment: introduction of the agent enriches the diet of a native predator, with impacts upon non-target prey (a more elaborate version of the shared predation module). (e) Intra-guild predation: the agent both competes with and attacks a non-target natural enemy.

Shared predation: identifying extinction risks for non-target prey

The 'shared predation' module focuses on situations where a natural enemy can attack two or more species of prey (Fig. 2.1a). A recognition of the potential importance of shared natural enemies has a long pedigree in entomology (e.g. Banks, 1955; van Emden and Williams, 1974). There is a large theoretical and empirical literature on the consequences of shared predation and parasitism for species coexistence (e.g. Holt, 1977, 1984, 1997a; Holt and Lawton, 1994; Begon and Bowers, 1995; Bonsall and Hassell, 1999; Courchamp *et al.*, 1999; Namba *et al.*, 1999). This module pertains very broadly, for instance, to: (i) a herbivore attacking two or more plant species (e.g. Louda *et al.*, 1997; Louda, 1998); (ii) a parasitoid attacking two or more host species (e.g. Müller and Godfray, 1999a); (iii) a hyperparasitoid sustained by two primary parasitoid species (e.g. van Nouhuys and Hanski, 2000); (iv) an internal pathogen capable of infecting multiple hosts (e.g. Thompkins *et al.*, 1999); (v) predatory arthropods attacking several prey arthropods (e.g. Karban *et al.*, 1994); (vi) vertebrate predators attacking vertebrate prey (e.g. Hoi and Winkler, 1994; Lawler *et al.*, 1998).

Structurally, there are three basic situations where risks due to shared natural enemies naturally arise in biological control:

1. Within a community, an introduced specialist agent may itself be consumed by resident generalist natural enemies. This does not directly match the labels of Fig. 2.1a, which refers to one agent attacking multiple target species, but is structurally similar in that there can be indirect interactions between species at one trophic level mediated through responses by a higher trophic level. If the introduced agent can be sustained at high abundance upon the target species, this could indirectly enrich the diet of resident natural enemies, which in turn then attack more effectively other resident prey or host species. An example of this effect has recently been reported by van Nouhuys and Hanski (2000). Experimental introductions of *Cotesia glomerata*, a parasitoid on pierid butterflies, were made into populations of the wasp *Cotesia melitaearum*, which parasitizes a nymphalid butterfly, *Melitaea cinxia*. This increased greatly levels of attack by a hyperparasitoid, *Gelis agilis*, even to the point of local extinction for *Cotesia*. Studies of natural host–parasitoid assemblages reveal that hyperparasitism is common (Müller *et al.*, 1999), providing a route for impacts of introduced specialist agents upon other species. Schönrogge *et al.* (1996) suggest that an additional risk of invasion by an alien herbivore is that it can enhance the abundance of native inquilines and parasitoids, thus placing at risk an array of native hosts. We are unaware of any screening programmes that assess the potential of this kind of risk factor in biological control.

2. Within a community, an agent may attack one or more species other than its putative target (see Fig. 2.1a). The danger of this effect is of course widely recognized (Howarth, 1990). What is not so widely recognized is that the magnitude of the danger posed to non-targets can be strongly influenced by the population dynamics of the target–agent interactions, and so will often involve indirect interactions among targets and non-targets. Below, we will use simple models to illustrate this basic point.

3. Risks due to shared predation can reach across habitat boundaries. Dispersal by introduced agents can couple dynamics of spatially segregated species. A habitat in which an agent interacts persistently with a target species can provide a source for immigration into nearby habitats with non-target but vulnerable species, or colonization into distant locales. The magnitude of these effects, once again, will depend upon the details of local population dynamics, as well as upon rates of spatial flows of individuals in heterogeneous landscapes. These effects can also be demonstrated with relatively simple models.

Disparate impacts of shared predation

Theoretical studies of the shared predation module suggest the following general, qualitative insight: the rate of attack by a generalist natural enemy upon a focal victim species depends upon: (i) the entire suite of victims sustaining that enemy, and more precisely their abundances, productivities and organismal traits relevant to attack rates; (ii) other aspects of population regulation; and (iii) the details of enemy behaviour. Because our concern is basically with the risk of species extinction, it is useful to concentrate on the conditions for a focal non-target species to increase when it is rare.

For simplicity, we will focus on situations where there is a single target species, and a single non-target species at risk. For a species with continuous generations, the per capita growth rate when rare can be described qualitatively (Holt and Lawton, 1994) by $r - a(N)P(N)$, where r is the intrinsic growth rate of the non-target species, $a(N)$ is the attack rate per enemy on the non-target species, expressed as a function of abundance of the target species, N, and $P(N)$ is the abundance of the control agent, which also depends upon the target species. [A technical aside: in actual models, predator abundance may not be expressed mathematically as a direct function of prey abundance, but it usually will indirectly depend upon consumption of prey and thus prey abundance, cumulated across predator generations.] For a species to be maintained in the community, one must have $r > a(N)P(N)$. All else being equal, one expects non-target species to be most at risk when: (i) the non-target has a low intrinsic growth rate (which makes it difficult for it to replenish losses); (ii) the natural enemy has high attack rates upon the non-target, even when the non-target is rare (this is most likely if the natural enemy is not easily satiated, or does not show switching behaviour; Murdoch and Oaten, 1975); and (iii) a high abundance of the natural enemy is sustained by the target species. The last effect is the key ingredient in *apparent competition*, the reduction in one prey or host species because of heightened attacks permitted by the presence of an alternative prey or host (Holt and Lawton, 1994).

Empirical studies of shared predation in biological control reveal a wide range of potential outcomes for shared predation. Sometimes, shared predation implies relaxed predation on each species. An example of this was described by Bergeson and Messina (1997) for lacewing (*Chrysoperla plorabunda*) predation upon two aphid species. Adding bird-cherry aphids (*Rhopalosiphum padi*) to treatments with predators increased the per capita growth rate of the Russian wheat aphid (*Diuraphis noxia*). Two crucial facts about this experiment are that the experimental treatment involved changes over short time periods, relative to predator generation length, and that the experiments were in a greenhouse, precluding predator aggregation from external sources. Predator numbers were thus fixed, and the only indirect interaction between the two prey was via behavioural responses by predators to the two prey types (e.g. saturating functional responses, switching, shifts in microhabitat use). In a follow-up study, Bergeson and Messina (1998) showed that non-target prey in the field also hampered the short-term effectiveness of biological control. In circumstances where predators have weak or negligible numerical responses, or where a study is conducted over short time-scales, one should often expect to observe indirect mutualism between alternative prey or hosts (Holt and Lawton, 1994).

In contrast, in a manipulative field experiment, Hanna *et al.* (1997) showed that a focal species, the Pacific spider mite (*Tetranychus pacificus*) was substantially depressed in local abundance by the introduction of a second species, the Willamette spider mite (*Eotetranychus willamettei*), because of a strong numerical response by the predatory Western orchard mite (*Metaseiulus occidentalis*). This study exemplifies a growing body of experimental work in field situations demonstrating the capacity of strong, indirect negative interactions between prey species sharing predators. For instance, a considerable number of recent studies have shown that the dynamics of aphid species utilizing different host species (thus precluding direct or exploitative competition) can be linked by shared natural enemies (Evans and England, 1996; Müller and Godfray, 1997, 1999a,b; Rott *et al.*, 1998). For instance, Müller and Godfray (1999b) showed that two species of aphids (*Aphis jacobaeae* and *Brachycaudus cardui*) were quite rare or absent during a long-term survey of a study site, despite their abundance in nearby habitats and availability of suitable host species. Using predator exclusion cages, they demonstrated that this local rarity was due to resident predation. Other experiments using direct manipulations of prey (Müller and Godfray, 1997; Rott *et al.*, 1998) suggest that this exclusion reflects numerical responses by predators to prey. The review by Howarth (1990) includes numerous examples in which it is reasonable to suspect that alternative prey, by sustaining predator populations, permit the suppression of focal prey species; hence, the indirect interaction between prey of apparent competition (Holt, 1977; Holt and Lawton, 1994). For instance, the coconut moth *Levuana iridescens*, endemic to Fiji, was driven extinct by the introduced tachnid fly *Bessa remota*: the fly is still common, presumably because alternative hosts are sufficiently available, though the taxonomic identity of the major surviving hosts on Fiji is unknown.

It should be noted that in some circumstances, the indirect interaction of apparent competition is essential for effective biological control in the first place. Settle *et al.* (1996) experimentally demonstrate that alternative prey, available throughout the year, help facilitate generalist predators in maintaining control of tropical rice pests, which are more seasonally pulsed. When a control agent is first established, its persistence may crucially depend upon its ability to utilize alternative species in addition to the target species (Obrycki and Kring, 1998). Moreover, a consideration of indirect interactions may contribute to the value of biological control in the first place. For instance, if the target species is a superior competitor, a natural enemy which selectively attacks that species can promote persistence of native inferior competitors (Mogi and Chan, 1997); this effect will be facilitated if the natural enemy can be sustained on these alternative prey. Indeed, indirect interactions between resident prey mediated through resident natural enemies may be a key factor in the ability of alien species to spread in the first place (Yela and Lawton, 1997). However, in this chapter our focus is on worrisome negative consequences of indirect effects of control.

Simple messages from theory

Message I

Even simple models illuminate different aspects of the potential negative impacts of shared predation. The first message we illustrate is: ‘intermediate levels of control may pose the greatest risk for non-targets’. In selecting control agents, one can readily assess attacks in controlled laboratory settings, without being able to predict effectiveness of control in the field. Consider a group of potential control agents consisting of relatively specialized predators. When introduced, each of these predators will attack a target pest species, but they vary in their effectiveness. Only one will be selected for introduction. Although relatively specialized, these predators can also incidentally attack a second non-target prey species, with negligible reciprocal effects of such attacks on the predator’s own dynamics. Given the large number of potential non-target prey species present in many settings, it is impractical to screen them all for vulnerability.

The impact of any of these predators upon non-targets should scale with the abundance of the predator, as sustained by interaction with the target prey. Assume that all these predators have a fixed per capita attack rate upon the non-target. Then, the total mortality imposed by the predator upon the non-target prey will be directly proportional to predator density. For a broad range of models, the maximal predator density sustained by a target prey density is realized at intermediate levels of control. A specific example of this effect is shown in Fig. 2.2, where we plot both q (an inverse measure of control) and P^* (predator abundance) as a function of per capita attack rate upon the target species for a prey-dependent Lotka–Volterra model. In general terms, when individual predators are highly effective at capturing the target prey, the predator population as a whole can more readily overexploit that prey; at equilibrium, fewer predators are then sustained by the target population. A predator that is very ineffective, of course, is unlikely to persist at all. The maximal predator population arises when individual predators have intermediate efficiency at capturing prey.

The basic reason for this effect is that equilibrial predator abundance tends to increase with total prey production, which in turn is maximized when prey numbers are at intermediate levels – neither near their intrinsic

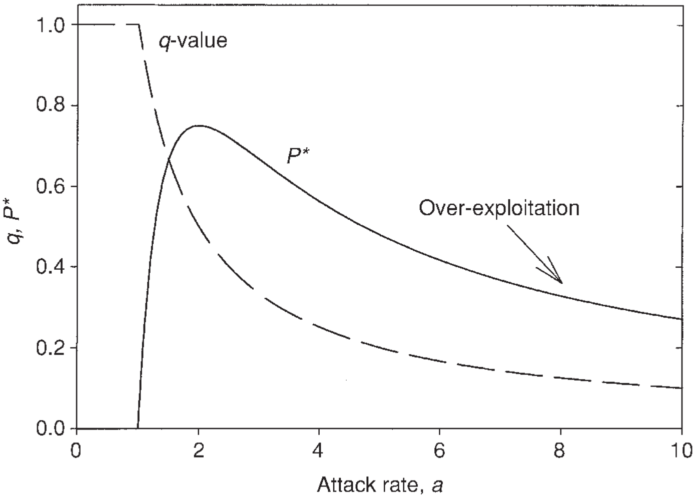

Fig. 2.2. A little control can be dangerous. The quantity $q = N^*/K$, where K is target carrying capacity (target abundance in the absence of control), and N^* is target abundance after control is established. The quantity a is the attack rate, per agent, per target. P^* is the abundance of the control agent (e.g. a predator). The example depicted assumes a Lotka–Volterra predator model, with logistic target prey growth and linear functional responses. At low attack rates, the predator cannot persist. At high attack rates, the predator overexploits its prey. Maximal predator abundance is observed at intermediate levels of attack, corresponding to intermediate levels of q.

carrying capacity, nor too near zero. In other words, predator abundance is maximized at intermediate control (e.g. $q \approx 0.5$) of the target prey. Hence, among our array of potential control agents, the greatest risk of incidental predation comes from those agents which are only moderately effective in control, because these are the ones that will not overexploit their prey. Murdoch and Briggs (1996), in reviewing models of specialist parasitoid–host interactions, suggest the following criterion for identifying an effective biological control agent: 'pest equilibrium density is suppressed most by the parasitoid species that needs the fewest host individuals to allow a female parasitoid to replace herself in the next generation'. A comparable rule-of-thumb for systems with multiple prey or host species is that the greatest indirect damage should be observed, for a given enemy–victim interaction, by that host species which can sustain the highest density of natural enemies (Holt *et al.*, 1994).

It is intriguing that reported cases of indirect agent impacts often do involve agents of intermediate effectiveness upon target species (see Lynch *et al.*, Chapter 6, this volume). We suggest that this tentative empirical generalization is consistent with existing predator–prey theory. And we caution that the above result has to do with predators with a fixed per capita attack rate on a non-target; agents with a high attack rate across all prey species will tend to overexploit all their prey, and so obviously should not be introduced in biological control.

Message II

The second simple message is that: 'measuring predator preferences does not suffice to estimate potential indirect impacts on alternative hosts/prey'. Assume that the predator can potentially persist on either the target or non-target species, taken alone, and that the two prey species have separate resource bases, and so do not directly compete. Let species 1 be the target species, and species 2 the non-target. Figure 2.3 shows results for a simple model. The model assumes continuous generations, spatially well-mixed prey populations, logistic prey growth, and linear functional responses to each prey taken separately or together (with no refuges from predation). The figure depicts how the conditions for coexistence of the two prey species vary as a function of the level of control of the target species (assuming the other species is absent). What determines persistence of the non-target is the value of a compound parameter, the ratio r/a, for the non-target, as compared with the target. If the non-target has the higher value for r/a, it will not be excluded. If the non-target has a lower value for r/a, then given effective control of the target species, the non-target is in danger of exclusion. If the predator can effectively limit the numbers of either prey species, considered one at a time, prey species coexistence is unlikely. Non-target species are vulnerable if: (i) one prey has a much

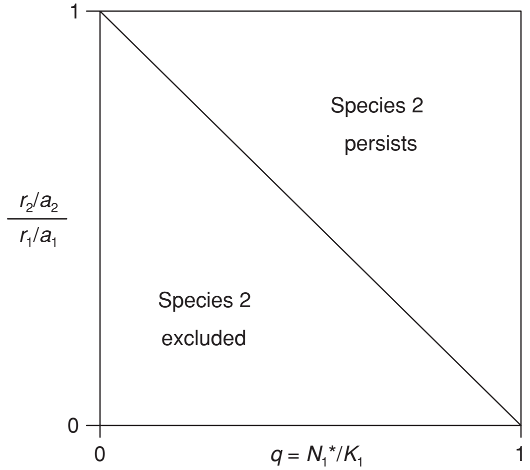

Fig. 2.3. Conditions for two prey species to coexist in apparent competition. The model (analysed in Holt, 1977) assumes logistic prey growth and linear predator functional responses. The quantity *r* is the intrinsic growth rate, and *a* is the attack rate. The quantity *r*/*a* can be interpreted as a measure of resistance by a prey population to predation, taking into account its ability to replenish its numbers via recruitment. We assume that prey species 1 has the higher value for *r*/*a*. Prey species 2 persists only if it has a sufficiently high value of *r*/*a*.

higher value for *r*/*a*; (ii) one prey type is particularly vulnerable to predation *a*; (iii) the prey species with higher *r*/*a* also has a high carrying capacity; and (iv) the predator is very effective on both prey species. Similar results arise in a variety of circumstances (e.g. alternative hosts for parasitoids (Holt and Lawton, 1994) or alternative hosts for pathogens (Holt and Pickering, 1985)). The simple take-home message is that knowledge of relative attack rates (preferences) alone is a poor guide to predicting the actual risk of the non-target species.

Message III

The third message is that 'field assessment of risk to non-targets concentrated in regions of high target abundance may underestimate risk in other conditions'. Apparent competition does not automatically occur whenever there is shared predation or parasitism. If: (i) predators easily saturate (or 'switch'); and (ii) predators experience strong density-dependence, for reasons other than via exploitation of prey, then alternative prey may experience indirect mutualism (because of a 'dilution' effect on predator attacks of alternative prey; Holt and Lawton, 1994). Figure 2.4 uses a graphical model to display this effect (after Holt, 1997b). The basic strategy is first to analyse the interaction between the target species and the control

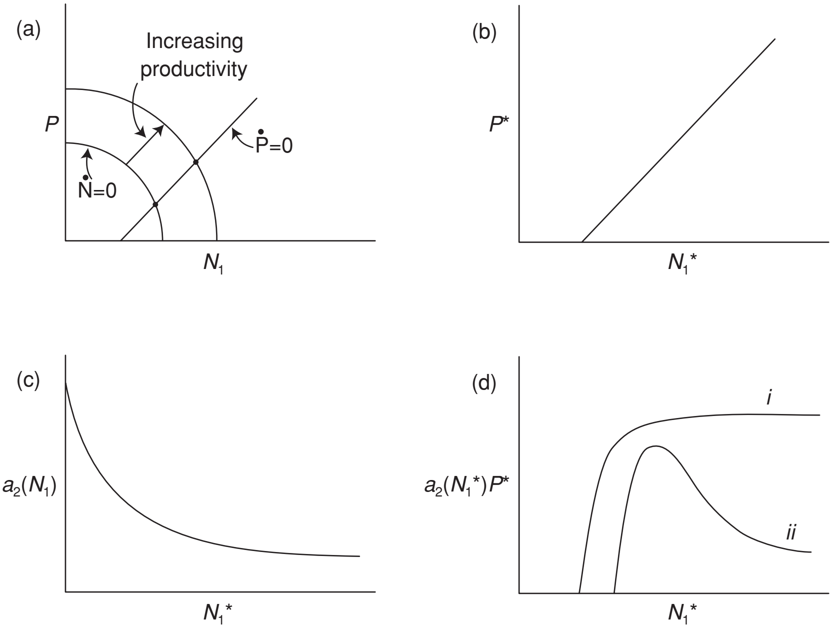

Fig. 2.4. A graphical model depicting complex interactions between prey species (modified from Holt, 1997b). (a) A standard isocline predator–prey model, with direct density-dependence in the predator; higher prey productivity pushes the prey isocline away from the origin. (b) As prey productivity increases, both N_1* (equilibrial prey abundance, for resident prey) and *P** (equilibrial predator abundance) increase. (c) The attack rate upon an invading prey species, per predator, per individual of the invading prey declines with increasing abundance of resident prey. (d) The *net* attack rate combines predator numbers and per predator attack rates. The former increases with resident prey numbers (see b), whereas the latter declines (see c). Overall predation is greatest at intermediate resident prey numbers. The magnitude of the 'hump' effect depends upon the details of the model (e.g. line *i* arises with small handling times, and line *ii* with large handling times).

agent, and then to evaluate potential impacts upon a second, non-target species, whose numbers are sufficiently rare that it does not influence the predator's own dynamics.

Figure 2.4a shows a standard predator–prey graphical isocline model, for a resident predator (the control agent) interacting with a resident target prey species. The target prey isocline is that combination of predator and prey densities where the prey has a zero growth rate. Because prey can compete for resources or otherwise experience direct density-dependence, there will be a maximal prey population size (its carrying capacity); this is the intersection of this isocline with the prey axis. The intersection of this isocline with the predator axis is the maximal number of predators that this prey could confront, and still persist. In more productive environments, one expects the prey carrying capacity to be higher, and the prey to be able to withstand higher predator numbers. If the predator can be satiated on this prey, then the prey isocline tends to bow away from the origin (and may even show a hump). From the predator's perspective, there will be some density of prey below which it cannot persist; this is the intersection of the predator isocline with the prey axis. If there are direct interactions among predators (e.g. interference or cannibalism) as predator numbers rise, there must be more prey for the predator population to remain in equilibrium; the predator isocline thus has a positive slope. The system equilibrates where the two isoclines cross. We assume that the presence of direct density-dependence in predator and prey suffices for the system as a whole to tend to remain stable. Given small environmental fluctuations, the equilibrium provides a reasonable approximation of time-averaged abundances. Thus, along a gradient in productivity, one expects to see increases in both predator and target prey numbers (Fig. 2.4b).

We now examine the impact of predation upon the non-target. Assume that the predator can be satiated, or has limited handling time. As target prey numbers rise, each individual predator's attacks will thus be diluted. Figure 2.4c shows how attacks, per predator, per prey, upon the non-target prey species should vary as a function of abundance of the target prey. If predator numbers were fixed, non-targets would enjoy lower predation pressure with higher abundance of the target species. However, given our assumptions, predator numbers should tend to rise with increasing target prey numbers (Fig. 2.4b). The net mortality (per prey) imposed on the target is the attack rate times the number of predators. In effect, we can multiply the relationships of Fig. 2.4b and c to produce Fig. 2.4d, which expresses the net rate of predation upon the non-target species (per individual of the non-target) as a function of the abundance of the target species. In general, one expects this relationship to be humped.

Over a given range of productivities, with little saturation and weak direct density-dependence in the predator population, the risk experienced by a non-target species tends to be greater if the target species has higher productivity (because this sustains the greatest number of natural enemies). However, if natural enemies readily saturate, and experience direct density-dependence (e.g. due to interference), the greatest risk to non-target prey may be associated with intermediate levels of productivity of the target prey. If the target population is sufficiently abundant, the agent may be limited by factors other than food availability (i.e. have a weak numerical response, thereby permitting indirect mutualisms, say because of saturating functional responses, to operate unchecked). Assessments of risk to non-targets, which focus on areas of high abundance of the target species, may underestimate risk to non-targets in areas with low target abundances. These realistic complications in predator–prey and other natural enemy–victim interactions may make it difficult to generalize across sites, even for the same set of species.

Indirect interactions influence transient risks during agent establishment

The above simple messages were derived from theoretical studies of models for shared predation, evaluated at a long-term stable equilibrium. Predator–prey systems are of course prone to strong oscillations in abundance, which can alter the expected direction of interactions among species in shared predation (Abrams and Roth, 1994; Abrams *et al.*, 1998). Moreover, all biological control systems involve a deliberate introduction, which means there is a transient phase of non-equilibrial dynamics as the agent increases in numbers, driving shifts in target and non-target species. Transient risks of extinction may arise during the initial phases of agent establishment and be aggravated by indirect interactions. A general feature of natural enemy–victim models is that a very effective enemy is expected to increase when rare, and overshoot its long-term equilibrial abundance (R.D. Holt, unpublished results). This implies that there may be a transient phase of intense predation upon non-target species, posing a risk of extinction even for non-target species able to persist with the introduced natural enemy in a long-term equilibrium (see also Lynch *et al.*, Chapter 6, this volume).

An example of this phenomenon is shown in Fig. 2.5. The example shown assumes the same basic model form as used for Fig. 2.3 (logistic prey growth, etc.). In this model, if two prey species have equal values for the compound parameter r/a, they are expected to have abundances in equilibrium with the predator that are proportional to their carrying capacities without the predator (Holt, 1984). In the example shown, the two prey species have equal carrying capacities and so should have equal abundances when in equilibrium with the predator. However, en route to this equilibrium the trajectories of two prey species can strongly diverge. The example depicted has prey species 1 with a higher attack rate than prey species 2, and a correspondingly higher intrinsic growth rate. Following introduction of the predator, its numbers rise while those of the two prey decline. The prey with higher a (species 1) experiences a long period of low densities, before gradually increasing with oscillations back to its expected long-term equilibrium. This highlights the importance of absolute attack rates in determining transient risks.

Numerical studies suggest that the pattern shown in Fig. 2.5 is generally observed in transient dynamics: effective predators can impose transient phases of extinction risk for prey as colonization occurs. Because of these transients, extinctions may occur due to demographic stochasticity at low numbers (an effect not captured in the deterministic model used to generate Fig. 2.5). As an introduced control agent moves across a homogeneous landscape with both target and non-target species throughout, there could be local extinctions of some non-target species in some locales, but not others, because of the chance vicissitudes of extinction risk during the

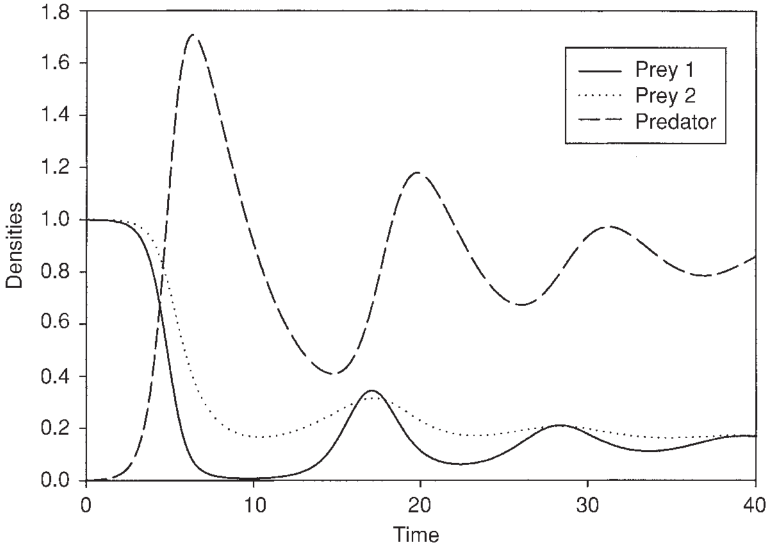

Fig. 2.5. A numerical example of transient risks of introduced natural enemies. The model is the same as in Fig. 2.3. The two prey have equal carrying capacities, and equal values for *r*/*a*, but prey 1 experiences a higher attack rate. The predator is introduced at time zero. At equilibrium both prey have the same abundance, but during the transient dynamics the species experiencing higher attacks suffers a disproportionate reduction in numbers.

initial phases of agent colonization. One long-lasting signature of transient dynamics may be great variability among sites in the realized community impacts of generalist control agents.

Landscape-scale indirect effects: the importance of community openness

So far, we have considered principally modules in local communities, for instance where a predator encounters each of several prey types during its daily foraging activities. There is increasing recognition of the importance of placing local community dynamics into broader landscape and even biogeographical scales (Ricklefs and Schluter, 1993). Useful insights come from examining community modules in a spatial context. In general, spatial segregation of species in heterogeneous landscapes promotes coexistence under shared predation (Holt, 1984; Bonsall and Hassell, 1999). However, following introduction, spatial flows of control agents from areas where control is desirable can potentially suppress non-target species in areas spatially removed from the focal control area. Such spillover, when it occurs regularly, in some ways is analogous to regular augmentation in biological control (May and Hassell, 1988).

Exclusion due to spillover through apparent competition can be illustrated with the following continuous-time Lotka–Volterra model, where it is assumed that the agent is present in a source habitat, and has a constant per capita rate of movement into a 'sink' habitat (with no back-flow, an assumption that greatly simplifies the algebra).

Source habitat dynamics:

Predator: $$\frac{\mathrm{d}P}{\mathrm{d}t} = P[abT - (e+d)]$$

Target prey: $$\frac{\mathrm{d}T}{\mathrm{d}t} = \mathrm{r}T(1 - T/\mathrm{K}) - aPT$$

Sink habitat dynamics:

Predator in non-target habitat: $$\frac{\mathrm{d}P'}{\mathrm{d}t} = P'[a'b'N - m'] + eP$$

Non-target prey: $$\frac{\mathrm{d}N}{\mathrm{d}t} = r'N(1 - N/K') - a'P'N$$

Here, P is the density of the introduced agent in the source, and T is the density of the target species. In the sink, P' is the density of the agent, and N the density of the non-target. The quantity eP is the 'spillover' of predators from target to non-target populations. We assume that without such regular immigration, the predator could not persist on the non-target species (i.e. $K' < m'/a'b'$). At equilibrium, the non-target host in the adjacent habitat is excluded (i.e. unable to increase when rare) if:

$$(e/m')\ (r/a)\ (1 - q) > r'/a'$$

where $q = T^*/K$ measures the effectiveness of biological control on the target species. Assume effective control (namely, q near 0). Exclusion of a non-target species due to predator 'spillover' from a habitat where the predator is sustained with a target species is more likely if: (i) the source habitat is more productive than the sink habitat (i.e. $r > r'$); (ii) the non-target prey is strongly attacked (high a'); (iii) predator movement rates are substantial (moderately high e; at very high e, predator numbers are depressed because of emigration); and (iv) predator mortality in the non-target habitat is low (low m'). Of these, (ii) and (iv) also make it more likely that the predator can successfully colonize and suppress the non-target prey, even without recurrent immigration. It is interesting that if $r = r'$, and $a = a'$, one can still see exclusion due to apparent competition 'at a distance' if $e > m'$. In analogous fashion, dispersal of the control agent out of the target habitat can lead to competitive exclusion of other natural enemies in other habitat, if the target habitat is sufficiently productive.

Transient dynamics in shifting landscapes

In heterogeneous landscapes, land-use changes can lead to transient phases of enhanced extinction risks. We will not examine this effect in any detail, but it is useful to consider a scenario where there is biological control established in a landscape with ongoing habitat destruction and fragmentation. If landscape change occurs rapidly, and predators are mobile and respond to a worsening environment by leaving, such movement permits predators to aggregate in the remaining habitat fragments. As with the introduction of predators in the first place, but to a more extreme extent, this leads to a transient spike in predator abundance in the recipient habitat, well above the numbers sustainable on the local prey base. As predators decline from this spike, there can potentially be a large reduction in prey numbers in the recipient habitat. In general, the impact of such transient dynamics on the recipient habitat will be greater if the source has a larger intrinsic growth rate or carrying capacity (R.D. Holt, unpublished results). The main conclusion is that landscape dispersal can lead to transient phases of high extinction risk due to an influx of enemies which attack prey found in the habitat fragments. This greatly increases extinction risks if the habitat fragments are low in the productivity of resident prey, and the predators are moving out of newly disturbed, productive habitats.

Finally, we briefly consider likely effects of shared predation at the scale of regional dynamics. Since the time of Huffaker (1958), it has been recognized that strong predator–prey interactions may persist because of metapopulation dynamics, wherein recurrent colonization balances local extinction (a kind of ‘permanent transiency’). Metapopulation dynamics can lead to prey exclusion in some habitats. Formal analysis of a metapopulation model of this effect is described elsewhere (Holt, 1997a). Here we just describe the main results. The basic scenario is that the landscape consists of a mosaic of two kinds of discrete habitat patches, separated by unsuitable habitat. For each habitat, there is a single species present and specialized to that habitat. One of these species is a target in biological control, the other is a non-target. An agent is introduced which effectively limits the target species’ local abundances, leading to local extinctions, but the agent can also exploit the non-target. The basic agent–target interaction persists because of metapopulation dynamics, with colonization balancing local extinctions.

A metapopulation by definition involves dispersal. Many organisms make mistakes during dispersal. Colonization by control agents into non-target habitats can increase extinction rates of non-target prey, reducing patch occupancy (the fraction of landscape occupied) of the non-targets. This can even lead to regional extinction. This indirect exclusion of one prey by another can occur even though the two prey species are never found in the same habitats, and even though predators are never found in empty habitats suitable for the excluded prey species.

Regional extinction of the non-target is particularly likely if the habitat it requires is scarce in the landscape, because this reduces the potential for recolonization following extinction. The risk of extinction of non-targets is also enhanced if the level of control by agents of targets is not sufficiently severe to risk local extinction (because this increases the fraction of the landscape which can harbour the predator), and if there is an intermediate level of exploitation in each target species patch (because this increases the local population size of predators, which increases the number of colonizing predators emanating from patches occupied by the target, ending up in patches occupied by the non-target).

The landscape of the modern world is becoming increasingly dominated by human activities, in particular by habitat destruction and fragmentation. Many species will in the future be restricted to scattered habitat remnants, surrounded by agricultural and other anthropogenic landscapes. Such species will be particularly vulnerable to indirect effects of biological control efforts, mediated by the spatial ‘spillover’ of agents into non-target habitats.

Indirect interactions and evolution

We have focused on the indirect ecological consequences of biological control. It should be stressed that comparable multi-species models are required to evaluate the potential risk of evolutionary host shifts, which could endanger non-target species which are currently safe. The direction of natural selection in the control agent will be channelled by the basic ecology of its interactions with other species, and in particular by the relative and absolute abundances of alternative hosts (M.E. Hochberg and R.D. Holt, unpublished results). Moreover, a control agent which has a large population size because it is only moderately effective at control will be able to harbour more genetic variation upon which selection can act to promote a host shift.

Conclusions

Theoretical studies of the ‘shared predation’ community module suggest a number of ‘rules-of-thumb’ which need to be considered when evaluating risks posed by introduced biological control agents:

1. A control agent which is only moderately effective at limiting target species numbers may be much more abundant than an effective agent, and thus pose a greater risk of incidental attacks on non-targets.

2. Given shared predation within a given habitat, the risk of extinction is enhanced for the non-target if it has either a higher attack rate or a lower intrinsic growth rate than the target species. The important message here is that measuring the magnitude of attack alone does not fully characterize risk to non-targets; species that have little capacity to replace additional losses (e.g. due to low *r*) are differentially at risk.

3. The risk to non-targets is greater if the natural enemy experiences little density-dependence due to factors other than its own resource availability (e.g. due to higher-order predators, or direct interference). The absence of such factors increases the number of predators, parasitoids, etc., sustained by a target victim species, thus increasing the exposure of non-targets to attacks.

4. The risk to non-targets is greater if predators have high maximal attack rates at high prey abundances (e.g. little satiation). This inflates the indirect effect of target species on non-targets, mediated through a shared natural enemy. By contrast, if predators readily satiate, alternative prey can experience indirect mutualisms.

5. If (3) and (4) both hold, the greatest risk to non-targets arises if target prey species can sustain high production in the face of predation (e.g. with weak predator density-dependence, increases in prey production can greatly increase both prey and predator numbers).

6. If, instead, (3) and (4) do not hold, the risk to non-targets may actually be greater at intermediate abundances of alternative prey. Considering realistic features of natural enemy–victim interactions (e.g. predator satiation, direct density-dependence) suggests that the same species pair could exhibit either positive or negative interactions, depending upon quantitative details of the entire suite of interactions in which that pair is embedded. This is a general feature of indirect interactions in complex food webs (Yodzis, 1988), and highlights the difficulty of devising simple theoretical predictions that will work in almost all circumstances.

7. Non-target species which can coexist with a control agent at equilibrium may none the less risk extinction during transient phases of agent establishment. During these phases, absolute attack rates may matter more than relative attack rates or reproductive rates.

8. Exclusion due to shared natural enemies can occur, even if target and non-target species never co-occur in the same habitats. This threat is particularly acute for non-target species which exist in habitat fragments commingled with the habitats occupied by target species, and when the agent is only moderately effective at limiting target numbers (i.e. no overexploitation) and the target species is highly productive.

9. Utilizing specialist natural enemies does not preclude all negative effects of shared predation, because such specialists can at times themselves be prey for resident generalist enemies. This is more likely to be of concern for some natural enemies (e.g. primary parasitoids, which can sustain hyperparasitoids) than for others (e.g. many internal pathogens).

We have focused on the shared predation community module, because this pattern of interspecific interactions is at the heart of recent debates about the dangers of biological control. We close by emphasizing that several other community modules exist (see Fig. 2.1) which isolate major avenues for indirect effects of biological control. All of these could be important in evaluating risks of biological control in some systems. Relating theoretical studies of modules to real-world control situations requires a thorough understanding of the natural history of one's system. Comparing theoretical studies of the different modules in Fig. 2.1 shows that the dynamics of a system can be qualitatively changed by adding or deleting a single strong interaction, or by altering the functional forms of relationships. It is difficult to evaluate the likelihood of this happening in general, but an awareness of how different module structures map on to different expectations of system dynamics is essential to understanding potential indirect effects of biological control. An understanding of the implications of indirect interactions in community modules should, we suggest, become part of the conceptual repertoire of biological control workers. Taking a 'modular' approach can help to crystallize one's understanding of core dynamical processes, which can then be discerned (if at times opaquely) in the working of complex communities (Hairston and Hairston, 1997; Belyea and Lancaster, 1999; Courchamp *et al.*, 1999; Persson, 1999).

Analyses of modules also suggest fresh hypotheses for empirical studies. When faced with the concrete details of real-world examples, failures in the match between theory and data provide pointers towards the development of a richer body of 'contingent theory' (Lawton, 1999), tailored to the specific details of particular communities. However, often one can discern the action of the broad forces identified in theoretical studies of modules in more detailed, realistic models. To mention one specific example, Schreiber and Gutierrez (1998) develop a realistic, physiologically based model of multi-species interactions in biological control and apply it to several biological control systems; the overall conclusions of their model (regarding competitive displacement) nicely match empirical outcomes observed in these systems, as well as the qualitative features of more abstract theoretical models. Finally, an explicit consideration of the population dynamic consequences of multi-species interactions is a necessary preamble to predicting the risk of evolutionary shifts from target to non-target species in biological control.

In closing, despite the risks of indirect interactions in biological control, aspects of which are explored in the above models, we wish to emphasize that biological control may often be the only reasonable approach to dealing with devastating pest problems (McFadyen, 1998). We hope that continued study, both theoretical and empirical, of community modules will help refine the long-term environmental soundness and sustainability of biological control efforts.

Acknowledgements

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3

Research Needs Concerning Non-target Impacts of Biological Control Introductions

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Abstract

Two workshops were held in 1999 on research needs concerning non-target impacts of biological control introductions. One took place on the Internet for 9 months, and the other in Montpellier, France, for 1 day. Altogether, over 200 researchers from over 30 countries participated, representing a wide variety of viewpoints on the issues involved. The deliberations of these workshops are summarized here. Both workshops highlighted the need for retrospective studies to: (i) identify cases of significant non-target impacts; (ii) explore mechanisms involved when such impacts are found; (iii) evaluate the reliability of host-range testing protocols; and (iv) determine whether and under what circumstances host ranges of biological control agents have evolved subsequent to introduction. Both workshops also emphasized the need for better understanding of the mechanisms underlying host specificity. Finally, both workshops recognized the desirability of collaboration among ecologists, economists, sociologists and biological control practitioners in research to assess and reduce the potential for non-target impacts of biological control introductions.

Introduction

This chapter summarizes the deliberations of two workshops: one sponsored by the Agricultural Research Service, United States Department of Agriculture, and held on the Internet during January–September 1999;

Evaluating Indirect Ecological Effects of Biological Control
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the other sponsored by the International Organization for Biological Control (IOBC) and held in Montpellier, France, on 20 October 1999, to conclude a 3-day conference on the subject. The Internet workshop was on research needs for assessing and reducing non-target impacts of biological control introductions. The Montpellier workshop was on research needs for evaluating non-target ecological effects of biological control, and thus was intended to cover not only introductions of exotic species but also biological control by augmentation and conservation of natural enemies. However, the emphasis was on non-target impacts of introductions for biological control.

Internet workshop on 'Research needs for assessing and reducing non-target impacts of biological control introductions'

Over 200 people from 28 countries subscribed to the mail-list through which the workshop was conducted; 49 participants posted 150 messages. An archive of these messages (with contributor names) is available at <http://www.udel.edu/entomology/khopper>. The emphasis was on arthropods introduced to control weeds and arthropods. Although there were a few postings on tangential issues (e.g. the biology of particular natural enemies, transgenic plants, the definition of biological control), most of the postings can be grouped under four germane topics: (i) what sorts of non-target impacts should concern us; (ii) host range evaluation; (iii) predicting impacts of biological control introductions versus other management options; and (iv) retrospective studies to assess actual impacts. The ideas summarized below are the contributions of 49 participants.

What sorts of non-target impacts should concern us?

Agreement is not complete on the species that should be considered when evaluating non-target impacts. Some have argued that impacts on all species should be considered equally; others hold that some species should receive special consideration (e.g. endangered species, species that provide crucial ecosystem services, species that provide economic benefits to society), and others hold that only such species should be of concern and impacts on others should be ignored. Although most agree that we should be concerned about population-level impacts rather than attacks on individuals, the magnitude and spatio-temporal scale of population-level impact that should concern us are not agreed upon. Depending on how impact is defined, its measurement may be extremely difficult. Field collection of hosts and exposure of sentinel hosts give impact on individuals which is hard to translate into impact on populations. Some argue that indirect impacts of arthropod introductions on parasitoids of non-target hosts may be larger than impacts on the hosts themselves. This is because parasitoids may be more liable to extinction than their hosts (LaSalle and Gauld, 1992; Unruh and Messing, 1993). However, such indirect impacts may be more difficult to measure than direct impacts on non-target hosts or prey. Not all impacts on non-target species need be considered detrimental. For example, introduced biological control agents might reduce the abundance of common native species that compete with or prey upon endangered native species, so that the introduction would decrease the extinction probability of the endangered species. Ultimately, the definition of non-target impact and how such impact is valued is a societal decision, but researchers attempting to evaluate non-target impacts need working definitions for design of surveys and experiments. Such definitions may be system specific, but it would be useful to agree upon guidelines for the sorts of impacts to consider.

Host range evaluation

Host range evaluation is usually the first, and often the only, step in predicting risks of non-target impacts. Some argue that the literature provides a good first screening for host range, especially for distinguishing candidates with broad versus narrow host ranges. Others argue that misidentifications in the literature, and especially the older literature, often cause problems of spurious host records. Some of these problems may be avoided by weighing the quality of literature data on host range, e.g. by taking into account numbers of individuals examined, percentage attack and spatio-temporal extent of studies. Laboratory or field experiments can be used to confirm data from field collections. However, physiological/behavioural host range measured in the laboratory and ecological host range measured in the field often differ. Host range evaluation in the area of origin can help with this problem by allowing comparison of field collections and laboratory measurements. An inherent assumption is that host range in the area of origin is a reasonably good predictor of host range in the area of introduction. Good design of experiments on host range usually involves system-specific factors. For example, the value of choice versus no-choice testing depends on the metapopulation dynamics of the system. If pests and non-target species commingle, or if a biological control agent can disperse from patches of pests to patches of non-targets, choice testing may be crucial. On the other hand, if biological control agents are likely to find themselves in areas without the target pest, no-choice testing may be more relevant. Some argue that host-range evolution poses significant problems for prediction of the host range of introduced natural enemies. Others argue that there is little evidence for host-range evolution after introduction, especially for herbivores introduced to control weeds (Marohasy, 1996). High levels of feeding and development on non-target species by a few individuals of a species may represent a greater risk of subsequent adaptation to the non-target than low levels of feeding or development by most individuals. This means that host-range testing should track the feeding and development of individuals and families. This will at least allow estimation of the likelihood of shifts in frequencies of genes/genotypes after introduction, although it will not provide information on the likelihood of novel genes arising. Ultimately, a deeper understanding of mechanisms affecting host specificity would allow better prediction of host ranges. Problems with host range screening of entomophages (difficulty of obtaining and rearing non-target species, problems with anomalous responses in the laboratory) may make such understanding particularly important for introductions against insects.

Predicting impacts of biological control introductions versus other management options

Host range testing is the most tractable approach to evaluating risks of impacts on non-target species. If one can show that a candidate for introduction will not attack any non-target species in the area of introduction, risk of non-target impacts is low. However, even in this case, indirect impacts may occur, e.g. if the target pest supports native species in some way. Furthermore, proving no potential for feeding or development on non-target species is difficult because one cannot test all possible non-target species and because host range may evolve after introduction. What is perhaps more important is that although many candidates for introduction have narrow host ranges, few are monospecific. The inclusion of species in the host range of an introduction candidate is often not simply dichotomous, with a list of species that are suitable for feeding and development neatly separated from those that are not suitable. Thus, several non-target species may be exposed to some reduced risk of attack compared with the target, and evaluation of the risks of significant impacts on these less suitable non-targets requires translation of attack on individuals to effects on populations. But there are major problems with predicting such impacts for target pests, let alone for non-target species. Furthermore, most agree that non-target impacts should be weighed not only against the value of controlling the target pest, but also against the risks versus benefits of other management options (Carruthers and Onsager, 1993; McEvoy, 1996; Simberloff and Stiling, 1996; Ricciardi *et al.*, 1998). If introductions are not made, resources devoted to other strategies may lead to increased biological control by natives (conservation, switching of generalists) or other successful control of the target. On the other hand, the pest may continue unabated and cause enormous economic or environmental damage. Unfortunately, we do not yet have the theory and methods that would allow quantitative comparison of the risks versus benefits of all management options. Although many debate whether we can develop methods for predicting which natural enemies are likely to be most effective, most researchers agree that pre-release studies in the areas of origin and introduction are needed to determine the value of controlling the pest, whether biological control introductions are likely to prove useful, and whether non-target impacts are likely. Mathematical models of the population dynamics of introductions may provide a common framework for comparing various systems and to handle the complexity of the potential interactions in most systems. The problem with modelling real systems is that so little is known that describing system structure, let alone estimating model parameters, may prove impossible at present and for the foreseeable future.

Retrospective studies to assess impacts

All discussion participants recognized the need for retrospective studies of previous introductions and their impacts. Such studies can provide the testing ground for predictions about non-target impacts, whether these are based on estimates of host range from field collections or laboratory experiments or on mathematical models of system dynamics. However, it is crucial to assess impacts in the light of host range testing and predictions made prior to introduction so that methods for assessing impacts prior to introduction can be evaluated. Releases have occurred when some level of attack on non-target species was possible, but considered less risky than alternatives for management of the pest (Kok *et al.*, 1992; Blossey *et al.*, 1994; Hasan and Delfosse, 1995; Hill and Hulley, 1995; Olckers *et al.*, 1995; Willis *et al.*, 1995). Impacts on non-target species and evolution of host range have rarely been evaluated for these cases in the past, but these introductions provide excellent opportunities for study. Some examples are:

1. *Chrysolina quadrigemina* feeding on *Hypericum calycenum*, an exotic plant extensively used as a ground cover in northern California, and on a native *Hypericum* species (Andres, 1985);
2. *Rhinocyllus conicus* introduced against *Carduus nutans* and feeding on non-target *Cirsium* spp. (Turner *et al.*, 1987; Louda *et al.*, 1997; see Gassmann and Louda, Chapter 8, this volume);
3. Biological control agents for introduced weedy *Solanum* spp. and feeding on aubergine *Solanum melongena* in South Africa (Hill and Hulley, 1995; Olckers *et al.*, 1995);
4. *Galerucella* spp. released against introduced *Lythrum salicaria* and feeding on native *Lythrum alatum* and *Decodon verticillatus* (Kok *et al.*, 1992; Malecki *et al.*, 1993; Blossey *et al.*, 1994);
5. An eriophyid mite feeding on native *Hypericum* species in Australia (Willis *et al.*, 1995);

6. *Tyria jacobaeae* introduced against *Senecio jacobaea* feeding on native *Senecio* spp. (Diehl and McEvoy, 1990);
7. *Diachasmimorpha tryoni* imported to Hawaii for fruit fly control parasitizing non-target tephritid *Eutreta xanthochaeta* imported for biological control of lantana in Hawaii (Duan *et al.*, 1997).

Several of these introductions are now being studied to assess non-target impacts, e.g. *R. conicus* (Turner *et al.*, 1987; Louda *et al.*, 1997; see Gassmann and Louda, Chapter 8, this volume), *Gallerucella* spp. (Malecki *et al.*, 1993) and *D. tryoni* (Duan *et al.*, 1997). But there are problems with the spatial and temporal scale of impacts versus our capacity to study introductions over large areas and long periods. All natural systems are dynamic, and introductions in particular may take a long time to reach equilibrium or at least a relatively steady state. Such dynamic systems present a moving target so that one may need to wait until an introduced agent is established over a broad area for a long time before evaluating the impacts of introduction. Ten years is often used as the time horizon for evaluating impacts of introductions on targets, but this is just a rule of thumb and may not even be applicable for target impacts, let alone non-target impacts. Such long time horizons and large spatial scales often put evaluations of target, as well as non-target, impacts beyond the resources available to most researchers. Unless thorough sampling was done before introduction, studying introduced species that have established over a large area for a long time means that potential control sites without the introduced species will be difficult or impossible to find. On the other hand, the slow rate of spread and patchy distribution of many introduced agents means that control sites without the introduced agent are often available long after introduction. A major problem with extensive surveys for non-target impacts is that negative evidence is hard to quantify and publish. Showing in a convincing way that small but significant impacts have not occurred is much more difficult and time-consuming than showing that large impacts have occurred. Although both conservationists and biological control practitioners regard with dismay illegal introductions and temporal and geographical differences in societal views about acceptable procedures for biological control introductions, differences in procedures do provide an opportunity to evaluate the effect of procedures on non-target impacts.

Montpellier workshop on 'Evaluating indirect ecological effects of biological control'

About 140 people from 26 countries participated in the Montpellier workshop (see IOBC, 1999, for a partial list of participants). The workshop was divided into two sessions. In the first session (1.5 h), participants were asked to develop and prioritize the major research questions concerning evaluation of non-target ecological effects of biological control. The participants were divided into 12 groups of 10–12 people, with a facilitator and recorder for each group. The facilitators moderated the group discussions, ensuring that all had the opportunity to participate in the discussions. The recorders noted down the salient points raised. In the second session (3 h) participants were asked to develop methods for answering one of the high priority questions identified in the first session. Each group was assigned a single question chosen by the workshop facilitators (Robin Huettel, USDA, Washington, DC, and K.R. Hopper, USDA, Newark, Delaware) from among the 36 highest priority questions identified in first session. At the end of the workshop, the group facilitators described the results of each group's discussion.

Session I: identification of major research questions

The workshop identified questions on: (i) predicting host range; (ii) predicting non-target impacts; (iii) evaluating non-target impacts; (iv) evaluating risks versus benefits of pest management strategies; and (v) reducing non-target impacts. The points from these questions are summarized below, although not necessarily in question format.

Predicting host range

The general question here is how to predict host range of biological control agents from information gathered prior to introduction. Host range in the source region is routinely used to predict host range in the introduction region, but how reliable are such predictions? Systematic and ecological affinities between target and non-target species were identified as major factors that can affect whether the latter would be attacked. But the reliability of such affinities in predicting host range needs more research. Retrospective studies on past introductions would be particularly useful here. Quarantine studies with species from the introduction region provide a means of directly measuring attack on potential non-targets. However, differences between physiological/behavioural and ecological host ranges, as well as abnormal behaviour under laboratory conditions, present problems for interpretation of quarantine research. Furthermore, rearing and measurement of large numbers of potential non-target species in quarantine may be prohibitively expensive. How can the predictive power of quarantine studies be increased and the costs decreased? Perhaps a better understanding of underlying mechanisms (physiological, behavioural, ecological, genetic and phylogeographical) that determine host range would enhance the predictive power of host range measurements prior to introduction, whether done in the source region or in quarantine.

Little is known about the frequency, rapidity or mechanisms of evolutionary shifts in host range. Yet such knowledge is crucial in determining whether measurements of host range prior to introduction will reliably predict post-introduction host range. Furthermore, knowledge of evolutionary mechanisms of host range shifts might allow predictions of such shifts, at least in cases where intraspecific variation in the biological control agent was implicated. Lastly, the usefulness of systematic and ecological affinities among target and non-target species, mechanisms underlying host range and the likelihood of evolutionary shifts in host range are all likely to vary between herbivores, parasitoids, predators and pathogens of plants and insects, and among taxa within these functional groups. How much of the theory and techniques from one group can be applied to another group?

Predicting non-target impacts

Here the general question is how to predict non-target impacts prior to introduction of biological control agents. If such predictions were reliable, one could introduce only those natural enemies with little or no likely impact on non-target species. Some non-target species may be more vulnerable to impacts of natural enemies than others, so prediction of impacts might include characteristics of the non-target species as well as those of the candidates for introduction. The amounts of dispersal by biological control agents into habitats with non-target species will greatly affect the potential for non-target impact. Thus, methods are needed for predicting where and how much biological control agents will disperse after introduction. As with host range, behaviour in the source region may provide insights about dispersal and habitat distribution in the region of introduction. As with evaluating impacts after introduction, predicting impacts requires decisions about magnitude, spatio-temporal scale and the hierarchical level of impacts of concern. Propagation of indirect impacts through ecological systems is a major area where knowledge is lacking. Retrospective studies may provide information about the likelihood of such propagation for various sorts of biological control agents and target pests. Furthermore, retrospective studies with particular biological control agents may provide information about the safety of these agents for future introductions.

Evaluating non-target impacts

Here the general question is how to evaluate impacts on non-target species, given that an introduced biological control agent is already established. First, we must decide which non-target species to study. Should these be beneficial, rare, keystone, beautiful or some other subset of the species in the introduction region? Given that the list of potential non-target species may be large and a reduced set may be necessary, how can sentinel species be selected? Some non-target species may be particularly vulnerable to certain kinds of attack or to attack at certain life-stages, so the choice of non-target species to consider will vary with details of the potential interaction. Choosing non-target species of concern implicitly ignores impacts at higher levels of organization, e.g. communities or ecosystems. Given a set of non-target species, communities or ecosystems of concern, we must decide which impacts to measure. Impacts will vary with hierarchical level (individual, population, community, ecosystem) and spatio-temporal scale. Impacts may be direct through feeding, competition or other processes, or impacts may be indirect through effects on food, enemies or competitors of intervening species. Impacts may also include changes in life-history or genetics of non-target species. Furthermore, economic, social and political impacts may be involved. Lastly, some impacts may be unanticipated: how can we design monitoring systems for these? Measurement of impacts will require comparisons, e.g. between conditions pre- versus post-introduction or between sites with and without the biological control agent.

Evaluating risks versus benefits

What level of impact should be considered significant? Related to this question is that of the magnitude of benefits that biological control agents provide. How do we quantify the risks and benefits (economic, social, political, environmental) of biological control agents versus pesticides/ herbicides and other alternatives for pest management? What common currency can be used for weighing impacts versus benefits of various management options? If stricter protocols are used for biological control introductions, what will be the economic and social consequences?

Reducing non-target impacts

Given that introductions of biological control agents will always involve some risk of non-target impacts, how can such risk be minimized? Reliable predictions of impacts on target species would help reduce impacts on non-target species by providing control with fewer species introductions. But how can predictions of impacts on target species be improved? If a biological control agent has established and been found to have unacceptable non-target impacts, how can such impacts be mitigated?

Session II: approaches to answering selected questions

How should we choose species to consider for non-target effects?

Lists of species to study for non-target effects could be developed by exclusion. Phylogeny, morphology, physiology, behaviour, geography, climate, phenology and habitat could be used as exclusionary criteria to delineate a subset of species that would be most at risk from a given agent. Various systems (e.g. marine, freshwater, terrestrial, weeds, insect pests) and methods of control (augmentation, introduction) would require different subsets of these criteria. For example, one would not use geography or climate as criteria for non-target species to consider under inundative biological control.

What determines host choice by an agent and what is the level of intraspecific variation in the determinants?

The sequence of behaviour that leads to host use has been broken into habitat finding, host finding, host acceptance and host suitability. Habitat finding can be affected by landscape structure, physical environment (e.g. light) and host plant effects (e.g. chemistry, morphology). These can be evaluated using literature data, field surveys, bioassays for tolerance/ preference, wind tunnels and olfactometers. Host finding can be affected by searching ability, experience and host cues. These can be evaluated with behavioural tests, dose–response analyses and patch use studies, all aided by mathematical modelling (e.g. dynamic programming). Host acceptance is affected by host physiology, chemistry, behaviour and age, as well as by previous experience of the natural enemy. These can be studied using electroantennography and behavioural assays, again aided by mathematical modelling. Host suitability is affected by physiological and humoral defences. These can be studied by measuring the mortality of natural enemy progeny, rate of encapsulation and host mortality. Each step in the process of host choice may vary among individuals within a species because of differences in experience or genetics. Genetic variation within and between populations in the traits underlying these processes can be studied with the techniques of quantitative genetics: family analyses, parent–offspring regressions, crosses and artificial selection. Molecular markers can also be used for mapping of quantitative trait loci.

How do we increase the predictive power of quarantine and other pre-release studies?

Increased predictive power is needed to improve confidence in protocols and risk assessments, while at the same time avoiding rejection of candidates that are actually safe. If possible, this increased power should not increase the complexity, expense or time required for risk assessments. Field tests of attack on non-target species in the source region should be pursued where possible. Genetic variation in host range of candidates should be determined and followed up with post-release studies to test whether host range has evolved. Predicted host ranges should be compared with actual host ranges after release to test whether the protocols worked. Molecular genetic characterization of candidates prior to introduction would allow tracking of introduced populations to ensure that non-target impacts were correctly attributed. Host range testing protocols might also be evaluated using accidental introductions or indigenous species, but it is not clear that the results would be applicable to carefully selected biological control agents. Long-term research on potential non-target species may improve the selection of species to study for non-target impacts.

How do we predict and detect host range expansion?

Lists of potential non-target hosts can be generated from literature data, field surveys and laboratory experiments. Ecological criteria for suitable hosts can be measured, including climate, potential natural enemies and competitors. Spatial analyses of data on distribution of the biological control agent in the source area could be used to predict where the agent is likely to occur in the target region. This information can be used to make statistical inferences about the potential for host range expansion. Predictions about host range should be tested with field studies of introduced agents. Here, one should collect data on population dynamics of the biological control agent and non-target species when together and separate (e.g. using cages, insecticides, geographical separation). Microcosms or plant assemblages could be used to study mechanisms of host range expansion. Various genetic strains of biological control agents and non-target species should be tested under a variety of ecological conditions (e.g. densities, alternative hosts) to determine the relative importance of ecological versus genetic constraints to host range. Lastly, if the molecular basis for host range were known, the likelihood of genetic changes in host range would be easier to infer.

How can host range testing be improved?

Considering only biological control by introductions and not augmentation or conservation, one could improve host range testing in the following ways. First, one should make results from host range testing available to others. Such results are often difficult to publish, but both positive and negative information about host range for each candidate is valuable, and should be made available either in the literature or in widely accessible databases so that it can be built upon. For each project, one should develop collaborative arrangements with others interested in the same targets and biological control agents or likely to be affected by the introductions. Such collaboration will minimize duplication, optimize resource use, overcome political boundaries, and thus both expedite and improve the safety of introductions. Because insects do not respect political boundaries, protocols should be harmonized among political jurisdictions that share biogeographical zones. At the beginning of each project, one should describe the systematics of the pest and biological control agents using the most advanced and appropriate methods available. Using information from the literature and from unpublished databases about similar taxa or ecological groups, one should rank the risks of non-target impacts of the biological control candidates. Using information on systematics and ecology, one should delineate actual host range in the source region and potential host range in the introduction region.

Laboratory testing may also be required; this could involve choice or no-choice experiments that give yes/no or graded responses concerning which taxa are attacked. However, the limits of laboratory tests must be recognized, and they should take into account the ecology of the interaction, e.g. the effects of host plants on parasitism of herbivores and the factors likely to affect female oviposition behaviour. Experiments should account for the possibility of evolution in host range. One might use artificial selection to develop candidates likely to have maximum impact on the target and minimum impact on non-targets. Although laboratory tests measure interactions at the individual level, one should keep in mind how these affect dynamics at the population level. Data collected in these experiments should be linked to theory and used to develop explicit models to identify key parameters. If the results suggest a low likelihood of attack on non-target species, one should progress to semi-contained releases to study population-level processes. Assuming favourable results here, one could then proceed to introduction and post-establishment monitoring programmes. Such programmes should be mandated and should continue for sufficiently long to evaluate non-target impacts. The results from these monitoring programmes should be made available in the literature or, if unpublished, in widely accessible databases.

How do we apply behavioural and physiological studies of host range in the real world?

A detailed answer to this question depends on the types of organisms; parasitoids and microbes would require different methodologies. However, a tiered approach should be used for any system. We already collect data on climate/microclimate, habitat/microhabitat and phenology of biological control agents and targets, as well as information on host finding, acceptability and suitability. We should collect such information for potential non-target species as well. This will reduce the risks of impacts on non-target species, while also preventing rejection of safe agents that may, for example, be able to develop on a non-target species, but would never encounter it in the field.

What constitutes acceptable risk in host range testing?

Acceptability of risk is a societal issue, which may evolve with changing societal values and scientific knowledge. Determining the acceptability of risk requires cost–benefit analyses that should include ecological and ethical issues, as well as economics. The decisions themselves are not scientific. However, science can provide inputs to aid in the decision-making. For host range testing the crucial issue is how to translate measures of host range to levels of impact on non-target species. An agreed upon scale to rank severity of impacts would be useful. We also need to maximize the information content of host range testing. This includes designing studies with sufficient statistical power and ecological relevance. The species tested should provide new information because the goal is to reduce uncertainty, so that one should not, for example, test aphid parasitoids against bees when one knows very well that the bees will not be attacked. To relate results of host range testing to likely non-target impacts in the field, one should conduct ecological and economic studies of potential non-target species. These would reveal the vulnerability of non-target populations to attack by the candidate and, if so, whether there would be other ecological or economic consequences. Retrospective studies are needed to determine the relationship between past host range testing and actual non-target impacts in the field. Large differences in biota between source and target regions may reduce risk of non-target impacts. For agents introduced to control insects, where host range testing has not been as thorough as for introductions against weeds, retrospective studies of host ranges in source regions compared with those in target regions would be particularly useful. Some types of biological control agents (e.g. generalist predators) may always represent too great a risk of non-target impacts and thus might be black-listed. Lastly, host range testing should also be designed to reduce the risk of rejecting effective and safe agents.

How can we predict spatio-temporal dispersion of biological control agents?

Observations and experiments in source regions could be used to predict spatio-temporal distribution in introduction regions. Observations would include determination of phenology and geographical and habitat distributions, including climatic and ecological characteristics. Dispersal could be measured directly or inferred from measurements of flight capacity or molecular genetic analyses of population structure. Studies on how alternative hosts, natural enemies and competitors affect reproductive rates in various habitats would delineate factors influencing spatio-temporal distribution that might differ between source and introduction regions. Experimental release of populations in marginal environments of the source region would help to determine the limits to distribution and their causes. Experiments on temperature dependence of development could improve our understanding of phenology. Measurement of movement into artificial infestations of target pests and movement out when target pest populations crashed could be used to explore metapopulation dynamics. Mathematical models could be used to synthesize these data to make predictions about spatio-temporal distribution in target regions. However, such predictions would require detailed information about climate, habitats, alternative hosts, and potential natural enemies and competitors in target regions. Predictions made prior to introduction should be tested with observations and experiments after introduction. This would require collection of data similar to that described above for the source region.

How can we determine the impacts on non-target species at the population level?

Assuming that non-target species of interest have already been identified, one should conduct long-term field studies of natural populations with and without the biological control agent. The studies should be long-term so that transient effects can be distinguished from more enduring effects. Comparison of non-target populations with and without the biological control agent could be achieved using pre- versus post-introduction dynamics, naturally occurring sites with and without the agent, or exclusion/removal manipulations. Each of these has problems, so it may be best to use a combination of them. The studies should be done in several ecoclimatic zones and replicated populations should be studied in each zone. To measure direct and indirect effects, one should follow the dynamics of the agent, a non-target species, and a natural enemy or competitor of the non-target species. Extension to more remote interactions would be too expensive. To reduce costs, one could begin by measuring incidence of attack. Above a chosen threshold of attack, one could start measuring population parameters. Sublethal as well as lethal effects may be important, but measurement of population-level impacts is the ultimate goal. Comparison of net reproductive rates with and without the agent over time would include sublethal effects and also address population-level impacts. If projections of further impacts were needed, data collected up to this point could be incorporated in mathematical models of population dynamics.

What are the risks versus benefits of biological control when compared with other control methods?

Three approaches could be taken to address this question: (i) a detailed case study or studies measuring all costs and benefits (ecological, social and economic) of all management strategies; (ii) prospective studies comparing in general the costs and benefits of various strategies and involving economists, sociologists and ecologists, as well as biological control researchers; and (iii) retrospective studies of past introductions to test how well costs and benefits were weighed. A major difficulty with detailed case studies is that measuring all costs and benefits of all management strategies may prove impossible or at least extremely difficult. Furthermore, a single case study or even several case studies would be difficult to generalize. Retrospective studies of introductions could indicate how risk–benefit decisions have been made. Such studies could address several questions: (i) What was known? (ii) What could have been known? (iii) Who made decisions and what was their expertise? (iv) What happened (i.e. what were the non-target impacts)? (v) What knowledge was gained (i.e. how were subsequent projects improved)? (vi) How do responses to the above questions vary with ecosystem, biogeographical province, political jurisdiction and decision-making framework?

Introductions for control of weeds may be most amenable to such retrospective studies because detailed petitions are available which summarize pre-release studies and include host testing information. For any of these approaches, a variety of variables must be considered. These include human health risk, environmental risks, development costs, risk of pest resistance, sustainability, selectivity, compatibility with other management strategies, and distribution of costs and benefits across society.

How do we identify and achieve an ecologically valuable community after introduction of biological control agents?

This is a difficult question in part because defining an ecologically valuable community is difficult and to some extent a societal matter. However, drawing on community ecology, we can outline some steps that would address the question. First, the community of interest should be described before and after introduction of a biological control agent. There are various descriptive tools available, including indices of diversity, measures of stability and food web structure. Also, one should identify and prioritize at-risk taxa and bio-indicators of ecosystem processes. What constitutes a desired or valuable community then would need to be defined by consultation among various segments of society, through workshops, public opinion surveys, etc. These would allow delineation of goals, e.g. concerning biodiversity and ecosystem functions. Such delineation might require further taxonomic or ecological studies. The outcome would be a set of performance indicators, which might include, for example, desired population levels and genetic structure of sentinel species, food web structure and farm profitability. The state of these performance indicators could then be monitored after the introduction of biological control agents. Such monitoring could include studies of the population dynamics and genetics of sentinel species and perhaps studies of the dispersal and field behaviour of the biological control agents. If the performance indicators were not in the desired ranges, then various methods of mitigation could be used. Mitigation could be guided by mathematical models developed from the information gathered during pre- and post-introduction monitoring.

How can we use retrospective studies to predict the safety of future releases?

The practice of biological control in general and of predicting non-target impacts in particular could be greatly improved by formulating testable hypotheses and then testing them. Examples of such hypotheses are:

1. The more intense the host range screening, the more predictable the non-target impacts;
2. Host specificity testing works for predicting direct effects but not for predicting indirect effects;

3. Direct effects are more likely for non-target species that are closely related to the target;
4. The more closely related non-target species are to target species, the more likely are non-target impacts;
5. Less specific biological control agents have more non-target impacts than more specific agents;
6. Non-target species in simpler communities are more at risk than those in complex communities;
7. Non-target impacts are a function of the inherent host ranges of biological control agents rather than other factors;
8. Effective biological control agents have fewer non-target impacts than ineffective agents.

To test these hypotheses, one should study a random subset of past projects, stratified using an ecological framework, e.g. by time since introduction, release rate and pattern, number of species introduced, number of species closely related to the target, community complexity and amount of host range testing done. The literature (e.g. Julien and Griffiths, 1998) and unpublished databases (e.g. BIOCAT, ROBO) would at least provide information about these variables and perhaps some information on non-target impacts. However, most of the data on non-target impacts would have to be collected in field surveys and experiments. Data on abundance, attack, mortality, and the biotic and abiotic environment could be collected in field surveys at the release points, the edge of current biological control agent distribution and beyond its current distribution. Collection of similar data in the source region might also prove useful. These data would need to be supplemented with results from field experiments to evaluate the actual impact of biological control agents on non-target species.

Conclusions

Although many of the same people contributed to both workshops, they represented a wide variety of viewpoints concerning potential for non-target impacts from biological control introductions. Both workshops highlighted the need for retrospective studies to: (i) identify cases of significant non-target impacts; (ii) explore mechanisms involved when such impacts are found; (iii) evaluate the reliability of host range testing protocols; and (iv) determine whether and under what circumstances host ranges of biological control agents have evolved subsequent to introduction. The workshops emphasized the need for better understanding of the mechanisms underlying host specificity to improve accuracy of predictions of host range. Although participants recognized the need to identify which non-target species and hierarchical levels of damage should be studied, they also agreed that such identification involves societal as well as scientific issues. Finally, the workshops recognized the desirability of collaboration among ecologists, economists, sociologists and biological control practitioners in research to assess and reduce the potential for non-target impacts of biological control introductions.

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4

Food Webs, Risks of Alien Enemies and Reform of Biological Control

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Abstract

As invasions of alien species mount, biological control will become an increasingly important tool of conservation and agriculture. In an effort to understand indirect interactions in biological control, we review food web ecology in terms of resource competition, trophic cascades, intra-guild predation, apparent competition, omnivory and a diverse set of tri-trophic interactions. The most inclusive study suggests that food webs in biological control are simpler than in natural communities. Risks to non-target species created by biological control have been studied seriously for only about 20 years, and knowledge of these risks is incomplete. The greatest risks are known to be posed by the organisms with the broadest diets, such as vertebrates and the snail *Euglandina rosea*, which has probably caused the extinction of an entire genus of native snails in Polynesia. Some parasitoid species have been introduced that are sufficiently polyphagous to attack native insects, and cases of serious harm to non-target populations are now coming to light. However, polyphagous organisms continue to be imported for biological control. One case in point is the campaign against the Russian wheat aphid, in which over 8.5 million individual invertebrates, including more than 1 million individuals of 12 species of ladybird beetles new to North America, were released over the past 15 years, with little study of potential non-target effects, direct or indirect. Another case is the new use of the polyphagous black carp for suppression of pest snails in industrial catfish ponds. This fish poses great risks to the high native diversity of molluscs in the Mississippi drainage. We argue that risk to native flora in

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biological control of weeds can be judged before introduction. For the New World, the lowest non-target risk comes from stenophagous insects released against weeds with no native congeners. When weeds have native congeners, introductions of even relatively stenophagous insects have led to the use of non-target, native plants.

Restraint is key to safe biological control. First must come judicious winnowing of potential targets. Not every alien species is a threat. Biological control is not the appropriate response to every pest, especially to native species perceived as pests. Second, not every available enemy promises relief. Importing multiple agents in a lottery search for one that might do the job increases the probability of non-target attacks upon the native biota. Restraint can come only from open discussion of risks versus benefits of biological control. What was the basis for the choice of the large number of imported enemy species in the campaign against Russian wheat aphid? What is the calculus of risk versus benefit in the dissemination of the black carp in the Mississippi delta?

Regulation of biological control in the USA is archaic. Oversight derives from a hotchpotch of old legislation designed to serve agriculture, and protection of native species under the current regulatory framework is deficient. Native invertebrates, terrestrial, aquatic and marine, are at greatest risk in the current structure, while native plants have had some, but not full, protection from foreign herbivores imported and disseminated for biological control. Although the ecological and economic value of invertebrates is not widely appreciated, these species are crucial to ecological integrity of our wild, urban and agricultural landscapes. Indirect interactions among native invertebrates can be threatened by alien species, and these contribute to the integrity of natural food webs. The sensible course is to extend Federal protection to minimize the risk to all native organisms. There is also a great need to pay attention to biological control organisms after they are released, and to restrict the propagation and re-release of those that can damage non-target organisms. With invasive species just as with many environmental issues, doing nothing is not neutral. Imported natural enemies are the last best hope to parry some of the most damaging exotic pests in natural areas as well as in agriculture. In the absence of reform, rational as well as irrational opposition to biological control will grow. Only sensible reform will maintain public support for this powerful tool.

Introduction

Biological control in conservation

There is nowadays a new effort to understand indirect interactions in biological control. Biological control has much to offer to conservation, management and restoration of ecosystems in these times of unprecedented rates of species invasions. Although the fact is poorly appreciated by the public (Colton and Alpert, 1998), invasive weeds are one of the greatest threats to natural areas. Suppression of weeds invading natural areas is the most prominent application of biological control currently employed in conservation. This practice grows out of the earlier use of weed biological control in range management and agriculture (McFadyen, 1998). A prominent example is the irreplaceable role of biological control in weed suppression in the diverse, precious and unique ecosystems of United Nations World Heritage Parks. In the South African Cape fynbos, invasive alien plant species are the greatest threat to the ecological integrity of the community (Olckers and Hill, 1999). Here, biological control is the only sustainable mechanism to suppress these invading weeds. In another World Heritage Site, the Kakadu National Park in Australia's tropical Northern Territory, some 89 species – or about 5% of the vascular flora – are invasive aliens, and these are judged to be threatening to the nature and conservation status of the Park. Biological control can make a substantial contribution to suppressing these invasive alien species both inside and outside of the Park (Lonsdale and Farrell, 1998). In the Everglades World Heritage Park in Florida, USA, biological control is in progress and planned against the most serious invaders, the Australian melaleuca tree (Center *et al.*, 1997) and Old World climbing fern (Pemberton and Ferriter, 1998). Biological control is also contemplated against insects invading natural areas (Frank, 1999), and even against invasive marine species (Clark *et al.*, 2000).

Food webs, direct and indirect interactions

The conceptual basis for integrating species interactions is food webs, the 'ecologically flexible scaffolding around which communities are assembled and structured' (Paine, 1996). The simplest kinds of interactions are direct, between pairs of species: competition, predation, parasitism, disease, mutualism. Indirect interactions involve more than two species and are the effects of one species passed via a second to a third species and to others (Menge, 1995). Perhaps the simplest kind of indirect interaction is competition between a pair of species that do not face off but that rely upon a common pool of living, depletable resources. An example of this resource competition in biological control is the suppression of native picture wing flies by the destruction of seeds of native thistles by the introduced *Rhinocyllus conicus* weevil (Louda *et al.*, 1997; see also Gassmann and Louda, Chapter 8, this volume). Another kind of indirect interaction, termed a trophic cascade, is the protection of a plant by a carnivore that suppresses a herbivore. This is the common goal of biological control of herbivorous insect pests (Hawkins *et al.*, 1999).

Intra-guild predation is a third type of indirect interaction, in which predators attack both the target species and other species, including other predators and other herbivores. The effects range from suppression of the pest, to no apparent effect upon the target, to the opposite outcome of that desired in biological control (elevation of densities of the pest). Moreover, intra-guild predation of generalist predators in biological control systems can lead to alternative stable states, unstable dynamics and to the generalist predator becoming extinct in the system (Holt and Polis, 1997). Recent research has shown intra-guild predation to be particularly pertinent to biological control (Rosenheim, 1998). Intra-guild predation, *ceteris paribus*, results in lower consumption rates of the target species than that by a single predator species alone. An example of intra-guild predation in biological control is *Zelus* bugs (Reduviidae) that feed upon both cotton aphids and lacewing larvae. The lacewing larvae are voracious aphid predators and, when alone, suppress the aphid populations deeply. Although *Zelus* bugs do eat some aphids, they have virtually no ability to control populations of the herbivore. By feeding upon the lacewing larvae, *Zelus* bugs disrupt the biological control of the aphid (Cisneros and Rosenheim, 1997). Another example of intra-guild predation, with similarly harmful effects upon biological control, is facultative hyperparasitism (Mills and Gutierrez, 1996).

A fourth kind of indirect interaction is apparent competition, in which one predator species feeds upon two prey species at different rates (Holt and Lawton, 1993; see also Holt and Hochberg, Chapter 2, this volume). Without knowledge of the existence of the predator, the changing densities of the prey would suggest that they were competing when they are not. An example of apparent competition that is *a propos* to biological control is one aphid species suppressed by a ladybird beetle species that was attracted to the area by the presence of a second aphid species (Müller and Godfray, 1997). In biological control, direct interactions are fairly well known, and indirect interactions are only beginning to be understood. Indirect interactions are much less obvious than direct ecological interactions, and it is only within the past decade, and only in a few systems, that indirect interactions are coming into clear focus. Omnivory is an element of trophic complexity that has led to a broadened concept of food webs for ecologists (Polis and Strong, 1996). In food web omnivory, a single consumer species feeds upon more than one kind of prey, for example, upon a predator species and simultaneously upon a herbivore species. In simple, linear 'top-down' chains of species, omnivory can destabilize interspecific relationships and lead to extinction of one or more species in the chain, while in more complex food webs – with reticulate interconnections – omnivory can lead to stability (Fagan, 1997). Stability is an important element of classical biological control, for maintaining suppressive pressure on pest species. Concern about food web omnivory has led to the notion of 'trophic spectra' with differently overlapping connections among omnivorous species. It has been argued that trophic spectra are a more accurate concept than discrete trophic levels for the relationships among the consumers and the consumed for many ecological communities (Polis and Strong, 1996).

Self-damping is an element of intraspecific interactions that is extremely important to the stability of interspecific interactions, to food webs and, thus, to biological control (Chesson, 2000). Theoretical work shows how self-damping affects the ability of a natural enemy to suppress its prey or host population (Levins and Schultz, 1996). In many cases, the impact of enemy species on average prey density varies inversely with the strength of self-damping. Predators with severe self-damping often have dynamics out of phase with prey numbers, leading to population cycling and reduced suppression of the prey population. An implication of this is that successful biological control requires a number of, rather than a single, species of agents that experience self-damping. Each of these species contributes modestly, and some uniquely in terms of environmental conditions, to the suppression of the pest. Generalist predators are especially likely to experience self-damping, and this insight complements the findings of Hawkins *et al.* (1999) that multiple predator species are the mode in natural regulation. Such multiple combinations of predators probably involve webs of interactions that would be difficult to create with introductions of generalist predators for biological control.

Cannibalism is a common form of self-damping for generalist predators, which are important entomophages in both natural and agricultural settings. Cannibalism is a doubled-edged sword for a predator. Consumption of close relatives can lead to loss of inclusive fitness and it carries risks of injury and disease transmission as a result of the prey being so similar to the predator. On the other hand, the commonness of cannibalism among general predators suggests very general benefits that would offset these costs. The rationale of theory of the benefits of cannibalism is that a competitor is eliminated while a meal is gained (Pfennig, 1997; Rosenheim, 1998). Cannibalism can increase as prey densities decrease (Pels and Sabelis, 1999), with the implication for biological control that alien generalist predators can have a particularly great influence in native food webs. Aliens that reduce prey density could increase cannibalism of native predators, and this could reduce the suppression of native herbivores.

Numerical and functional indirect interactions are other elements of food webs that are germane to biological control. Numerical indirect interactions are the simplest sort and those that are most readily modelled. In these, per capita rates of growth and consumption are unaffected by the physical presence of other species: predator species do not avoid each other or otherwise affect each other's behaviour. Numerical indirect interactions include those of general predators that consume the aphid mummies made by a parasitoid in the system (Ferguson and Stiling, 1996). Functional interactions are qualitatively different from numerical ones.

They are more complicated. Functional interactions include behavioural changes in a predator and/or prey caused by the perception of the presence of the other species (Lima and Dill, 1990); for example, the prey species that refrains from foraging when sensing the presence of a species of predator (Schmitz *et al.*, 1997). Induced resistance of plants by one herbivore species that results in poorer performance of another herbivore species (Karban and Baldwin, 1997) can be considered a functional indirect interaction. Janssen *et al.* (1998) argue that mite food webs illustrate well the issues of numerical and functional indirect interactions and that the more complex functional indirect interactions are important for biological control involving mites. Compared with natural communities, the mite food webs are not rich in species, while at the same time they are not impoverished in kinds of interactions. Even the fairly simple food webs with mites are reticulate; they are food webs rather than food chains: complex interactions such as apparent competition, intra-guild predation and resource competition are very much a part of the picture to be expected in biological control. This suggests that as our knowledge of other biological control communities increases, equally rich sets of interactions could reveal themselves.

Finally, the rubric ‘tri-trophic interactions’ is useful for tying in the additional, important kinds of food web effects that do not fit into the neater categories discussed above. Examples include consumption of introduced biological control insects by native species (Pearson *et al.*, 2000), plant manipulation of natural enemy behaviour (Vinson, 1999), simultaneous nourishment of both natural enemy and herbivores in an elaborate form of omnivory (Baggen *et al.*, 1999), influence of a diverse plant community upon the suppression of a herbivore by a parasitoid (Messina *et al.*, 1997), and the reticulate effects of fungal endophytes of plants upon the attack rate upon herbivores by natural enemies (Grewal *et al.*, 1995).

Combined effects of different biological control agents upon the same species, target as well as non-target, are a sort of tri-trophic interaction worth contemplating. An example is insect-vectored plant pathogens, which could magnify both the damage and the number of species attacked beyond that of the herbivore or the pathogen alone. This scenario is approached in the biological control of thistles in North America. Both *R. conicus* and *Trichosirocalus horridus*, which attack non-target native thistles, can vector *Puccinia carduorum*, an introduced rust disease of weedy thistles. Fortunately, the rust did not infect the non-target, native thistles tested in laboratory and field studies (Bruckart *et al.*, 1996). This situation bears watching because the insects may vector the rust to other, possibly susceptible, native thistles. The levels of innoculum reaching non-target thistles could be greater than what would arrive through aerial transmission alone. If combined, herbivore–pathogen effects can enhance the damage to target weeds; they could also increase non-target effects.

Differences between natural and cultivated systems

Ecologists have a fair knowledge of indirect interactions in a few systems. Some of the best known are among algae and invertebrates in the rocky intertidal (Menge, 1995), among plankton and fish in some lakes (Carpenter and Kitchell, 1993), and among lizards, spiders and prey insects on small Caribbean islands (Schoener and Spiller, 1999). Most analyses of indirect interactions are based upon a subset of species that are obvious or otherwise accessible to researchers while the remainder of the food web is less well known. Analyses of these subsets have been termed ‘interaction webs’ (Menge and Southerland, 1976), and more recently ‘community modules’ (see Holt and Hochberg, Chapter 2, this volume). The ecological dynamics of modules can be understood as a mathematical network of interactions, and the analyses of modules have yielded ecological insights about the potential for indirect interactions to affect communities. In nature, community modules are connected to yet other species by interactions that are only poorly known, and knowledge fades at the edges of modules into a form that is reminiscent of a vignette. These lesser-known influences can affect the dynamics of the module. Understanding how modules fade into vignettes is a way of taking account of our ignorance (Strong, 1999).

Risks of biological control

A discussion of the risks of biological control to native species, both direct and indirect, is meant to foster sensible means for dealing with these risks. The enthusiasm of advocates can exceed the need for biological control, and without sufficient care it can misfire. The use and harm to native species by some introduced biological control agents has led to questions about the safety, rationale and even the need for some projects (Miller and Aplet, 1993; Civeyrel and Simberloff, 1996; Simberloff and Stiling, 1996; Hager and McCoy 1998; Lockwood, 1999). In this section we will assess some of the most prominent risks of biological control, acknowledging that some risks may yet be undiscovered or at least under-appreciated. At the same time, we have emphasized in the introduction that biological control is a valuable tool for conservation as well as for agriculture. Balancing the benefits against the risks is the task at hand. In the final section we will suggest steps toward reform that will reduce the risk to native species and environments. Reform is necessary for sustaining the public trust in this powerful technique.

While classical biological control has been practised for more than 100 years, focused scholarship on non-target effects is only about 20 years old (Andres, 1980; Howarth, 1983). From the inception of this sobering literature, vertebrates have been flagrant, bad actors. The polyphagous nature of vertebrates almost always makes them unsuitable for biological control. One poignant example is the cane toad, *Bufo marinus*, introduced to Australia in 1935 in an abortive attempt to biologically control introduced insect pests of sugar cane (Burnett, 1997). It has spread to occupy over 0.5 million km^2. It continues to spread linearly at about 40 km year^{-1} and by leap-frogging, as in the recent arrival of cane toad in Western Australia (Callaghan, 2000). Unlike Australian amphibians, this tropical American toad is exceedingly toxic and can kill Australian predators that attempt to eat it. Snakes, goannas (*Varanus* monitor lizards), birds and carnivorous marsupials such as the small quoll possum, *Dasyurus hallucatus*, are especially at risk. The high populations and indiscriminate, large appetites of cane toads lead to wholesale consumption of small, native ground-dwelling vertebrates and invertebrates (Niven, 1988). Other vertebrates causing distinct non-target effects include the Indian mongoose, *Herpestes javanicus*, which is inferred to have caused the extinction of several native reptiles on Caribbean and Pacific islands (Honegger, 1981). In a manifestation of the indirect interaction termed 'apparent competition', feral house cats and red fox feed primarily upon introduced rabbits and house mice, and with this dietary subsidy maintain populations that threaten native marsupials and birds in Australia (Groves and Burdon, 1986; Risbey *et al.*, 1999).

In a criticism of mentioning the past errors of vertebrate use, some biological control researchers have asserted that the cases discussed above are just 'stories from the past'. However, consider the polyphagous, alien grass carp introduced into the USA in 1963 for the biological control of aquatic weeds and still used widely (Julien, 1992; Bain, 1993). In response to a similar accusation that raising the issue of the cane toad is 'hysterical' and 'alarmist', consider the current legislative climate in the state of Mississippi, USA, which is encouraging biological control of snails in commercial catfish ponds with the alien black carp, *Mylopharyngodon piceus.* This fish is a generalist consumer of molluscs, and poses a substantial risk to native clams and snails in the Mississippi drainage and beyond (Nico and Williams, 1996; Nico, 1999). This area is a centre of biodiversity for freshwater molluscs, especially unionid clams (McMahon, 1991; Stein *et al.*, 2000).

Emphasis upon the ecological safety of biological control has increased in the last 15 years (Pemberton, 1985a,b; Turner, 1985). Many of our presently serious non-target problems of biological control are being caused by agents introduced when attitudes were tilted in favour of agriculture and when dangers to native species were discounted or even ignored. (However, note that the case of the black carp indicates that risks from attitudes that discount the environmental harm of biological control are very much with us in the new millennium.) Thus, in 1957, the voracious Argentine caterpillar *Cactoblastis cactorum* was introduced to the Caribbean, without regard to the rich native *Opuntia* flora in perilously close continental North America. Appearing in Florida in 1989, either as an introduction of the nursery trade or as a natural migrant (Pemberton, 1995), *C. cactorum* now attacks five native Florida opuntias, including the rare semaphore cactus (Johnson and Stiling, 1996). Likewise, in 1968, the weevil *R. conicus* was introduced from Europe for control of weedy thistles, even with evidence in hand that it might feed upon native North American thistles. Now widely distributed, it feeds upon the seeds of at least 22 native thistles, including several that are rare (Louda *et al.*, 1997; Pemberton, 2000; see also Gassmann and Louda, Chapter 8, this volume). Perhaps the most egregious harm from biological control followed the 1977 introduction to the Pacific Island of Moorea of the predatory land snail *E. rosea*, from Florida and Central America. This failed attempt to control the giant African snail instead caused the extinction of seven species and perhaps the entire endemic genus of *Partula* snails (Murray, 1993). This generalist predator has also harmed native snail fauna of other Pacific islands (Cowie, 1998).

What of the risks of indirect effects of non-target attacks in biological control? We argue that, although not much is known on this topic, the potential risk of indirect harm to native species is great. The classical theory of a nature comprised of short unbranched food chains in which indirect interactions were limited to trophic cascades (Hairston *et al.*, 1960) has been replaced by theories of reticulate food chains rich in possibilities for indirect effects. In modern theories, the results of food web interactions depend upon the details of linkages between species (Polis and Strong, 1996). Newer ideas of multiple predators, herbivores and plant species, variously cross-linked, complement the simpler, original idea of the generality of the trophic cascade. Insect predators are often attacked by yet other predators. The implication is that the actions of biological control agents are contingent upon the other species in the food web (Rosenheim, 1998). Biological control agents commonly have interactions with entomopathogenic viruses, bacteria, fungi and nematodes, as well as with a range of insect predators and parasitoids. These intra-guild predators, resource competitors and community mutualists can have a great influence on the effects of consumers. Food webs are a frontier of ecology, and the science of non-target effects of biological control agents in food webs is in its youth.

Weed biological control

The science of predicting risks is much more advanced for the biological control of weeds than for insects. This statement is based upon a general assessment of the risk to non-target, native plants posed by insects introduced for biological control with data on field host use of 112 insects, three fungi, one mite and one nematode established for biological control of weeds in Hawaii, the continental USA and the Caribbean against 55 weed species since 1902 (Pemberton, 2000). Of the 112 species of insects introduced for biological control, 15 use 41 native plant species, 36 of which are congeneric with target weeds, while four others belong to two closely allied genera. Only one of 117 established biological control organisms uses a native plant unrelated to the target weed. This demonstrates that virtually all non-target risk is borne by native plant species that are closely related to target weeds. Thus the elements of protection for the native flora are the selection of weed targets that have few or no native congeners and the introduction of biological control organisms with suitably narrow diets.

Insect biological control

The risks to native insects and other invertebrates caused by biological control are poorly known compared with those for weed biological control (Ehler, 1998; Jewel *et al.*, 1999). The potential expense to agriculture and other industries of non-target uses of plants by agents introduced for weed biological control has always been great, and attention to avoiding non-target economic damage has a long history (even if this attention has only recently been applied seriously to protecting wild native plants). While attention to ecological safety is increasing in some quarters of insect biological control (Ehler, 1998), it is far from universal and often ecologically unsophisticated (Lockwood, 1999). Another important consideration is that insects are inconspicuous, and lists of potential native, non-target species are difficult to establish and woefully incomplete. Most native insect faunas are poorly known and there has been insufficient interest in non-target insect species. A big element in the poor development of safety for entomophages is that insects and other invertebrates have far fewer advocates than do plants. With the exception of pollinators, they have little immediate commercial value, and society has an extremely poor appreciation of the ecological value of insects.

Parasitoids and general predators

Most of the known non-target attacks upon native insects are attributable to introduced parasitoids, which leave more distinctive evidence than do predators (Funasaki *et al.*, 1988; Barratt *et al.*, 1997). While a lack of taxonomic knowledge of most parasitoid groups hinders the resolution of the data (Memmott, 1999), we do know that scores of introduced parasitoid species attack native insects (Hawkins and Marino, 1997). Although non-target effects are poorly known, parasitoids introduced long ago can harm native herbivore populations today (Boettner *et al.*, 2000). While some parasitoid species are extremely narrow in their host range, some generalist predators occupy the opposite end of the spectrum and have the ability to attack many native species where they are introduced. The most general of predators have a number of prey species, which can vary with life history stage, with the seasons, and with the place of foraging as these vary with life history and season.

Trophic relationships between entomophages and hosts or prey are more diverse than those between herbivores and plants. In an inclusive statistical analysis of 68 life tables of introduced and native insects, Hawkins *et al.* (1999) showed that biological control of insects results in less reticulate trophic relationships than those in natural food webs of native insects. For native generalist predators, food web reticulation and complex interconnections are the mode for suites of multiple interactions between native insects, herbivores and plants. Suites of generalist predators utilize each prey species, making suppression of a herbivore a joint effort. The analysis, based upon literature records, found that the reticulations of native food webs contrast with the mode in biological control in cultivated habitats in which single introduced parasitoid species control single exotic insect herbivores on exotic plants. The cases included in the analysis concerned species of insect herbivores for which at least five generations or a combination of five generations and sites of life table data were measured. Although measured key factors are not necessarily the only influences upon temporal variation in population, they are the best available means for synoptic, general assessment of direct influences of a consumer upon a resource population. The key factors were classified as either parasitism, predation, disease or 'other' causes. The category of other causes included items such as decrease from maximum fecundity, migration and competition with other herbivore species. Some studies revealed more than one key factor, and the assessment included a total of 80 key factors for the 68 life tables.

An implication from Hawkins *et al.* (1999) was that the sort of biological control of insect herbivores that most frequently succeeds in agriculture is not a 'strictly natural phenomenon'. The short linear food chains of biological control differ from native entomophagous food webs, in which the modal pattern is reticulation of trophic relationships. This is not to say that strong, single-species links with one enemy species controlling one resource species do not exist, because good examples are known (Schmitz *et al.*, 1997; Moran and Hurd, 1998). However, this statistical evidence of complex links in natural food webs complements a literature that proposes that more diverse communities are tied together by multiple trophic influences among species (Strong, 1992; Polis and Strong, 1996).

In native systems, generalist predators and polyphagous parasitoid species contribute a substantial amount to control. The dynamics of natural systems are a result of multiple links in food webs, many of which are overlapping and individually much less forceful than the links in cultivated systems. This is consistent with the idea that populations of native predators rely upon a series of prey species, perhaps in a series of habitats, rather than upon a single prey species in a single habitat. It is also consistent with the notion that in persisting and being available at the right time and place to prey upon a herbivore, the generalist predator is ‘subsidized’ by a range of other prey species. One can term this kind of polyphagous, subsidized existence for general predators a kind of omnivory. It can operate within life history stages or between them, with larvae relying upon different prey species from adults of a generalist predator (Polis and Strong, 1996; Rosenheim, 1998).

The elements and facets of native arthropod communities that we have discussed above indicate substantial complexity of food webs and trophic linkages. It is this complexity into which biological control agents are introduced. Unanticipated consequences follow from unanticipated complexity, and a prime example is given by the now-discontinued programme of biological control of native rangeland grasshoppers in North America (Goodwin, 1993). Among the non-target species likely to be affected by the proposed programme was the native grasshopper *Hesperotettix viridis*, which feeds primarily upon snakeweed species, *Gutierrezia* spp. Snakeweeds are among a group of poisonous native plants that cause great losses to cattle that ingest them (Lockwood, 1999).

Ladybird beetles

Ladybird beetles are particularly germane to issues of indirect interactions and non-target effects in biological control (Obrycki *et al.*, 1999). As of 1985, 179 coccinellid species had been intentionally imported to the United States, 16 of which appear to have become established (Gordon, 1985). Additional ladybird beetles have been imported since then. Five alien ladybird beetles are generalist feeders that have dispersed through substantial portions of North America. Their spread has been hastened by efforts to propagate and introduce them to new areas for the purposes of biological control of pest aphids. The diets of alien ladybird beetles in North America are diverse: some are restricted to mites and others to scales, while still others specialize upon mealybugs, and many are generalist predators. They range among different habitats and feed upon a range of prey species. They can consume prey species that are in the diets of native entomophagous species, such as diets of native ladybird beetles that can be involved in natural biological control of native herbivore species. Consistent with their designation as generalists, the prey of generalist coccinellid beetles is defined less by taxonomic relatedness than by size, location on the plant and habitat.

The introduced ladybird beetles raise red flags of particular risks to the multiple relatively weak links in natural communities. Obrycki *et al.* (1999) observe that although the data are not particularly good, the current diversity of coccinellid species in parts of the Midwestern USA appears to be lower than that shown in studies before 1950. While the declines certainly could be the product of the multiple habitat changes and even changed climate, one focused study suggests otherwise. Patterns in what was judged to be a pertinent habitat variable – reduction in the lucerne crop over a 18 year period – were uncorrelated to the change in the structure of the coccinellid communities (Elliott *et al.*, 1996). Competition and intra-guild predation with introduced coccinellid species are more likely causes of the decrease in diversity of the native coccinellids. It has been noted by other authors that competition with native generalist predators from introduced general predators can be a greater risk to biological diversity than to the prey of the introduced species (Simberloff and Stiling, 1996; Samways, 1997). Propagation and spread of previously introduced ladybird beetles could contribute to attacks upon native insects. Examples include the seven spot and *Harmonia axyridis* ladybirds which are general predators that consume a wide variety of prey as well as the pest aphids that are their targets (Obrycki *et al.*, 1999).

The campaign against Russian wheat aphid

New entomophagous species with broad diets continue to be introduced into North America. A case in point is the campaign against the Russian wheat aphid, which introduced 29 new species of general predators, and parasitoids, and two new forms of two fungi species to 16 states between 1986 and 1993 (Anonymous, 1993; Quisenberry and Peairs, 1998). The programme bred and released over 8.5 million individuals, including more than 1 million individuals of 12 species of ladybird beetles new to North America. Although some research on the biology of these species was carried out during the programme, a philosophy of first studying candidate enemy species was rejected in favour of collecting and releasing as many species of potential enemies as quickly and in as many sites as possible (Prokrym *et al.*, 1998). At the same time '. . . few sound criteria and techniques were available for making such choices' (Hopper *et al.*, 1998). The rationale was urgency felt for the need to control this pest (Prokrym *et al.*, 1998). One evaluation of the campaign was that the limited evidence available indicated that the introduced natural enemies have had little influence upon densities of Russian wheat aphid in the USA (Hopper *et al.*, 1998). Another evaluation (Prokrym *et al.*, 1998) was that any assessment of efficacy was hampered by the limited information gathered. It was difficult to distinguish taxa believed to have been released from native North American species and species released previously, and the scientists worked without adequate biological or ecological information. Prokrym *et al.* (1998) ventured the opinion that biological control of a pest aphid on an annual crop in vast acreages of monoculture was not bound to succeed. The literature on control of Russian wheat aphid is large and diverse, and of the 200 publications we have reviewed, some 60 indicated an interest in biological control. The number making reference to non-target effects of introduced enemies of the Russian wheat aphid is quite small, however. In addition to those cited above, one can add Elliott *et al.* (1994) and Hammon and Peairs (1998). With the caution that we probably have missed some literature, it is fair to say that not much is known about non-target effects of these alien predators and parasitoids, because little was invested in understanding the potential to harm the native North American biota in the campaign against the Russian wheat aphid.

Reform of biological control

Restraint is the key to safe biological control. Judicious winnowing of potential targets comes first. Not every invasive species is a threat, and not every pest is appropriate for biological control. Native organisms are the riskiest of targets. Even pestiferous natives can have substantial and complex ecological roles. Natives are linked by trophic interactions to other natives. The discontinued biological control programmes against mesquite, *Prosopus glandulosa*, and against rangeland grasshoppers (Lockwood, 1999) illustrate the issues. First, for society as a whole, the pest status of these is equivocal. Though both are a problem for some ranchers, both are also substantial components of native communities, with trophic links to many other species. This means that biological control could cause unexpected indirect effects. In contrast, the balance of benefit to risk of biological control against native insects that attack row crops, including corn rootworm, cotton bollworm and Colorado potato beetle, is much greater because of the very great economic value of these crops and the large amount of insecticide that biological control replaces in these cases. However, we hasten to caution that introduced enemies of native pests of row crops can harm other native species that are not pests. Our society has invested very little in the science of understanding collateral damages to native insects caused by biological control agents, and this is an important area for future research attention by both general ecologists and the biological control community. For these reasons, we suggest that native organisms should be targets for biological control under only extreme circumstances. When they are, special study of collateral effects is needed.

Not every available natural enemy promises relief. The continuing tendency to import multiple agents in a sort of *post hoc* lottery search for some or even one that will do the job increases the probability of non-target attacks upon the native biota (McEvoy and Coombs, 1999). It also justifies the judgement that some biological control is ill advised or misdirected. What is the scientific basis for the choice of the particular enemies and for the large number of enemies in the campaign against Russian wheat aphid? Were all 29 newly introduced foreign species needed? What was the expected benefit of each species relative to its risk to the native biota? We suggest that weighing evidence of efficacy should be part of all biological control projects, in an effort to import the fewest foreign enemy species possible.

The basis of ecological safety in biological control is suitably narrow diets of agents. For weeds, the statistics show that native plants most closely related to the target weed have the highest risk (Pemberton, 2000). Thus, the safest targets are weeds without close native relatives in the region (Pemberton, 1996). A good example is tamarisk, a species complex of trees from Eurasia that invade natural wetlands and watercourses throughout the south-western USA. Tamarisk plants deplete surface water and displace natural vegetation such as cottonwood, willow and mesquite. Notwithstanding the possibility that some macroevolutionary insect herbivore shifts can be mediated by plant chemistry not revealed by plant taxonomy (Becerra and Venable, 1999), it is proposed that an ecologically safe insect herbivore for control of tamarisk plants in America need only be restricted in diet to the family *Tamaricaceae*. This is based upon the fact that the western hemisphere lacks natives in this plant family (Deloach *et al.*, 1996).

Many pests, however, do have native relatives in areas where they have been introduced, meaning that the diet of an agent must be suitably narrow, so as not to threaten natives. For example, even the relatively stenophagous herbivores of European thistles are not sufficiently specific to prevent their adoption of a number of the 90 native North American *Cirsium* thistle species. Five biological control agents have been introduced against *Carduus* thistles and two are known to use native thistles. Current knowledge is that *R. conicus* now uses 22 of the 90 native *Cirsium* in the USA (Pemberton, 2000). What is to prevent *R. conicus* from using additional native North America *Cirsium* spp.? For example, the Sacramento thistle, *Cirsium vinaceum*, Woot. and Standl., in New Mexico is a good host in the laboratory, but the weevil has not yet spread into its range (R. Lee, personal communication). The weevil *T. horridus* feeds upon the native *Cirsium discolor* (Muhl. ex Willd.) Spreng. in Virginia (McAvoy *et al.*, 1987) and could probably use other *Cirsium* spp. because it attacks rosettes, which are available over all or most of the season. By contrast, *R. conicus* is restricted in host use to the flower buds of *Cirsium* spp. that are available during its oviposition period (see Gassmann and Louda, Chapter 8, this volume).

The greatest attention to safety has been with the biological control of weeds because collateral damage to agricultural plants is expensive. The United States, like all but a few countries, has no laws created specifically for biological control. Old statutes barring alien species harmful to agriculture have been applied to regulate importation of agents against weeds. Regulation is in the hands of the Animal and Plant Protection Service of the Department of Agriculture, guided by the Federal Plant Pest Act of 1957, the Plant Quarantine Act of 1912 and the Noxious Weed Act of 1974. In recent years, protections have been extended to native plants, consistent with The National Environmental Policy Act of 1970, which requires Federal activities to consider possible environmental effects. The Animal and Plant Health Inspection Service review begins with a evaluation petition submitted by a scientist. Petitions are then reviewed by a Technical Advisory Group ('TAG'), with members representing different resource interests within the Federal government. If the Technical Advisory Group recommends approval, the petitioning scientist submits an application for a release permit through his or her state department of agriculture. The Animal and Plant Health Inspection Service then prepares an Environmental Assessment. If there results a 'Finding of No Significant Impact' ('FONSI') and the US Fish and Wildlife Service which consults on the Environmental Assessment concurs, a release permit is issued. We suggest that a review process like this, with important changes, is a good template for improved practice. The changes should include external expert review of petitions and a more transparent process such as posting of the petitions, the external reviews and Technical Advisory Group recommendations on the Internet. The appropriate government agency for the regulation of biological control should be chosen after national discussion of these issues (Anonymous, 1995).

Most native insects, mites and other invertebrates lack the key combination of legal regulatory protections afforded to plants from harm caused by biological control introductions. Although the ecological and economic value of invertebrates is not widely appreciated, these species are crucial to the ecological integrity of our wild, urban and agricultural landscapes. Their lack of protection is alarming because of their substantial role in nature (Strong *et al.*, 1984). Native herbivorous insects and mites control plants that could become pests in the absence of this natural control. Invertebrate predators, parasites and parasitoids control herbivores, both native and alien, that could severely harm vegetation. Indirect interactions among native invertebrates, which can be threatened by alien species, contribute additional glue to our natural communities. Neither evidence of efficacy nor that of safety is required for introduction of organisms that have insects and mites as targets. The US Animal and Plant Health Inspection Service has no clear authority to exclude species other than those that threaten plants, pollinators and established biological control organisms, except by invoking the National Environmental Policy Act. However, neither state nor other non-Federal activities are regulated by this Act.

The sensible course is to extend protection to all native organisms, with carefully chosen exceptions made for the small number of unequivocally serious native pests. The current US Animal and Plant Health Inspection Service review for weed biological control is a good model: we recommend that a process of petition and expert review is the legal avenue required for all biological control introductions, herbivorous and carnivorous alike. All proposed introductions should meet stringent criteria of need, appropriateness, efficacy and ecological safety. Is the proposed target a serious pest or does it threaten to become one? Is biological control the appropriate approach to control? Is the proposed agent sufficiently harmful to suppress the pest? Is the proposed agent safe? The evidence on safety should define the probable risks to native and other valuable species by means of data on hosts or prey in the native, origin area of the candidate as well as results of rigorous host-prey specificity and range testing. The *ad hoc* Technical Advisory Group review should be open and include experts from the spectrum of appropriate government, university and private organizations. Finally, there is need to more carefully regulate propagation, re-release and movement of biological control organisms after their introduction. The issuance of an Animal and Plant Health Inspection Service permit for release is usually the end of effective Federal oversight. While states can regulate movement of an agent, usually they do not. With few exceptions, state regulators defer to judgement of USDA–APHIS about the safety of agents for their state. ‘Safety’ usually concerns agriculture and not native organisms. This means that, once in the USA, the knowledge that native species are threatened by a biological control organism serves for little in preventing its propagation and spread. For example, in the case that no native molluscs were threatened or endangered, the Endangered Species Act could not be invoked, and little if any effective Federal regulatory impediment could be brought against the dissemination of the black carp among catfish farms. How likely is escape of this voracious mollusc-feeder into the Mississippi drainage? Likewise for movement of alien ladybird beetles which threaten native predacious insects; for *R. conicus* which threatens native thistles; and for *C. cactorum* which threatens native and commercial *Opuntia* in Mexico and the USA.

Introduced natural enemies do not respect political boundaries. Increasing the general ecological safety of biological control in the USA could provide guidance for the more challenging international implications of this technology. Important examples include agents released in Canada that migrate to the USA, and *C. cactorum* which, now in Florida, could move into Mexico to threaten the large industries based on *Opuntia* there. The spectre of *C. cactorum* moving west from Florida to attack 60-odd species of native *Opuntia* in the USA and south to attack the native and commercial *Opuntia* in Mexico illustrates how biological control is both a national and an international issue. Some of the most threatening invasive species are marine, and biological control is being contemplated as one technique for dealing with these aliens. Most oceans span boundaries and nations will soon need to address the transborder issues of marine biological control (Bax *et al.*, 2000). Countries are responsible for their own regulation of biological control introductions into their territory. The ecologically motivated reforms discussed here (the appropriate use of biological control, for a carefully selected subset of pests, and the utilization only of natural enemies with suitably narrow diets) will, however, reduce the risk of biological control to non-target native organisms everywhere.

We suggest the following additional guidelines to assist the management of biological control:

1. The practice of biological control should be separated from its regulation.
2. The participation of different resource-based government agencies (i.e. environmental protection, agriculture, forestry, fisheries, etc.) should be encouraged in decisions on biological control.
3. External review and comment should be part of the process.
4. The process should be transparent to the public. Information relating to proposed introductions, safety testing and decision-making can be posted on the Internet and in other appropriate media.

We also suggest that guidelines for reducing the risk of biological control to non-target native organisms, perhaps incorporating the ideas discussed in this chapter, be considered to strengthen the United Nations FAO 'Code of Conduct for the Import and Release of Exotic Biological Control Agents' (FAO, 1996; Greathead, 1997). With invasive species just as with many environmental issues, doing nothing is not neutral. Imported natural enemies are the last best hope to parry some of the most damaging exotic pests in natural areas as well as in agriculture. However, in the absence of reform, opposition to biological control – rational as well as irrational – will grow. A few sensible steps such as those that we suggest herein will maintain public confidence and support for this powerful tool for use against invaders of natural areas as well as in agriculture.

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5

Evaluation of Non-target Effects of Pathogens Used for Management of Arthropods

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Abstract

Entomopathogens can be used in classical, conservation and augmentative biological control. For the most part, entomopathogens have been developed as microbial insecticides for inundative augmentation, although there remains great potential in using them with inoculative augmentation, classical and conservation approaches. Ecological effects of microbial control agents on non-target organisms can come about either through direct infection of the non-target organisms or through indirect effects, principally depletion of the target population. Direct effects can be avoided or minimized by careful selection of highly host-specific pathogens. In inundative biological control, both direct and indirect effects are usually reversible even when pathogens with a broader host range are used, effects that have been documented are minimal and pathogen levels eventually return to background levels following application. Permanent indirect effects could be possible if an exotic or genetically engineered pathogen were to become established and provide long-term control of the target host. Such indirect ecological effects may be minimal if the target population has been introduced in the first place. Of course, it could be very undesirable if endemic target invertebrates were affected. To date there is no evidence of detrimental ecological effects from deliberate introductions of entomopathogens for use in 'classical' biological control. Insights into possible side-effects can be obtained from studies on natural epizootics of indigenous strains. Most studies of detrimental effects of entomopathogens have centred on pathogens being used inundatively. In these

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cases, although direct impacts on non-target invertebrates closely related to the target host are common, there is little evidence to suggest that these pathogens become established in populations of non-targets, thereby causing long-term effects. Even though there are numerous possible direct and indirect effects of microbial pesticides on non-target organisms, in the end it must be realized that it is generally not possible to manipulate one part of the ecosystem without in some way affecting other components (i.e. any control efforts will have impacts, as would nothing).

One of the main reasons for reluctance to use entomopathogens in biological control has been that protocols and methods for evaluation of the potential risks of introductions of entomopathogens were lacking. There has also been great reluctance in releasing genetically modified entomopathogens for similar reasons. Protocols for registration and release of genetically modified organisms are becoming available and several such entomopathogens have now been released, with no evidence of detrimental ecological effects. However, such protocols rely almost exclusively on laboratory studies, many of which may provide meaningless information, as far as prediction of long-term detrimental ecological effects is concerned. A better understanding of basic pathogen and target host ecology and epidemiology is needed in order to better predict potential detrimental effects. Long-term studies of entomopathogens already registered and in use could provide models for risk assessment. The development of better and more pertinent evaluation methods and protocols is also needed. When evaluating the risk posed by microbial control agents, whether they are applied inundatively or in the classical sense, it is important to include in the risk analysis the alternatives to not controlling the pest, i.e. the devastation to non-target organisms caused by depletion of food resources, competition with aggressive pests or effects of the use of broad spectrum chemical treatments.

Introduction

A broad spectrum of microorganisms causes diseases in arthropods. Basic interactions between these different species of microbes and their arthropod hosts determine which hosts are infected. First, infective propagules of pathogens must contact potential hosts and next, pathogens must be able to enter the host's body and evade or overcome immune defences. Which host species actually become attacked in nature can be influenced by any of these steps and differs for different pathogen species. Some pathogens are very host specific. For example, the host range of grasshopper entomopoxviruses is generally limited to host species within the same subfamily (Lange and Streett, 1993). In contrast, some pathogens have a relatively broad host range. For example, the entomopathogenic fungus, *Beauveria bassiana*, has been recorded from over 700 arthropod species, including numerous hosts that are not pests (Goettel *et al.*, 1990). However, due to variability within pathogen species, individual isolates of any pathogen are usually much more host specific than the species as a whole. Pathogens have very different methods for infecting hosts, e.g. pathogenic bacteria, viruses and protozoans must be eaten by hosts and then invade through the gut wall. Most fungal pathogens penetrate directly through the cuticle and species of pathogenic nematodes use both methods for infection. Following recent convention, we will include arthropod-attacking nematodes in this discussion, although it could be argued that many of these act more as parasites than as pathogens.

Entomopathogens can be divided into two broad categories: obligate and facultative. Obligate pathogens require a living host in order to complete their development. In general, these pathogens are well adapted to their host, are highly virulent and have a narrower host range. Obligate pathogens are often known to cause spectacular epizootics within host populations. In contrast, survival of facultative pathogens is not dependent on a living host. Facultative pathogens are generally less virulent, have wider host ranges and are opportunistic.

Types of control

Entomopathogens can be used in classical, conservation and augmentative biological control. For the most part, entomopathogens have been developed as microbial pesticides for inundative augmentation, although there remains great potential for using them in inoculative augmentation, classical and conservation approaches. While inoculative augmentation and conservation could also have non-target effects, conservation is fundamentally different because it is not based on release of natural enemies in the environment but, instead, on manipulation of habitat or management practices. Inoculative augmentation and conservation have been explored relatively little (but see recent reviews on conservation by Fuxa, 1998; Lewis *et al.*, 1998) so we will concentrate our discussions on techniques involving inundative and classical use of pathogens for pest management.

Classical biological control

Classical biological control, the release of an exotic natural enemy for pest control, has been used little with entomopathogens. Over 2000 species of insect parasitoids and predators have been released for control of insect pests (Greathead and Greathead, 1992) while in contrast, less than 50 exotic pathogens have been released (Fuxa, 1987). In some instances, releases of pathogens have been accidental but have resulted in excellent control. Among the relatively few exotic microorganisms released, some have demonstrated great promise. Pathogens used for classical biological control generally are extremely host specific and have great potential to persist in the environment and cause epizootics. The ability to mass-produce these microbes is not critical because generally only small amounts of inoculum are released. We will briefly describe several of these examples of successful releases.

Entomophaga maimaiga *and* Lymantria dispar

Lymantria dispar was introduced to north-eastern North America in 1868 or 1869 and, by the turn of the century, this insect was recognized as an important forest defoliator whose populations had great potential to spread (Liebhold *et al.*, 1989). This pest is native from Europe across temperate Asia. In 1909, a fungal pathogen, *Entomophaga maimaiga*, attacking *L. dispar* in Japan was collected and brought to the Boston area. Releases of this fungus made in 1910–1911 were not thought to have resulted in establishment (Speare and Colley, 1912). In the 1970s to 1980s, pathogen surveys of *L. dispar* populations were conducted but *E. maimaiga* was never found until huge epizootics occurred across seven north-eastern states during the extremely rainy spring of 1989 (Hajek *et al.*, 1995b).

Between 1989 and 1992, *E. maimaiga* spread across the contiguous north-eastern distribution of *L. dispar* in North America. Due to the rapid spread of *E. maimaiga* between 1989 and 1992, it is highly questionable whether the strain of *E. maimaiga* present in North America since 1989 is the same as that released in 1910–1911 or is perhaps a more recent accidental introduction (Hajek *et al.*, 1995b). Regardless of the source of the fungal strain, *E. maimaiga* was the principal natural enemy causing declines of *L. dispar* populations in central New York in 1992. Host populations throughout the north-eastern USA predominantly remained low until at least 1999, with continued infection by *E. maimaiga* in very low density populations (Hajek, 1997; A.E. Hajek, unpublished results). Although many biological control introductions have been made against *L. dispar* in North America (Hoy, 1976), this fungal pathogen is unique due to the high levels of infection it has demonstrated in both high and low density host populations. *L. dispar* outbreaks in North America are characteristically unpredictable and, while none has occurred since *E. maimaiga* was first found, more time is necessary before the long-term impact of this pathogen on this outbreak insect can be predicted.

Non-occluded virus and Oryctes rhinoceros

The palm rhinoceros beetle, *Oryctes rhinoceros*, occurs throughout south-eastern Asia but was accidentally introduced to many South Pacific countries as well as Mauritius (Bedford, 1981). This beetle can cause severe damage or mortality of palms, including those species producing coconuts and oil. A virulent non-occluded virus (a virus not contained in a proteinaceous matrix referred to as an occlusion body) was first discovered in

O. rhinoceros larvae native to Malaysia. This virus was subsequently mass-produced in insects and then distributed by inoculation into breeding sites (artificial log heaps) from which beetles auto-disseminated the pathogen. The virus established well after releases in many island groups and consistently caused significant reductions in beetle-induced damage. This virus has little effect on larval survival, but is thought to be so effective because viral infections reduce the longevity of adult beetles and the virus can persist well at low host densities (Zelazny *et al.*, 1992). The economic benefits of this programme have been estimated at a cost:benefit ratio of > 1 : 100 (C.J. Lomer and H. DeGroote, personal communication).

Therioaphis trifolii *and* Zoophthora radicans

The spotted alfalfa aphid, *Therioaphis trifolii*, was first found in Australia in 1977, causing severe damage in lucerne. The only fungal pathogen attacking this aphid in Australia had negligible effects on populations of this species. Virulence of a diversity of isolates of the entomophthoralean fungus *Zoophthora radicans* was compared and an Israeli strain isolated from *T. trifolii* was selected for release. The first field releases were made in 1979 (Milner *et al.*, 1982) and the pathogen became established and spread. By 1986, the pathogen had spread across New South Wales and southern Queensland. As a result, *Z. radicans* frequently causes epizootics in late summer and autumn and, because activity of *T. trifolii* is seasonal, only the first aphid populations in early summer are likely to escape infection (Milner, 1986). Other control measures were simultaneously developed, including introduction of the parasitoid *Trioxys complanatus*, which this pathogen does not infect (Milner, 1986).

Beddingia *(=* Deladenus*)* siricidicola *and* Sirex noctilio

Monterey pines (also known as radiata pines) from California were introduced to Australia, where they thrived and became the primary species in commercial plantations. In 1952 and 1961, the European woodwasp, *Sirex noctilio*, was accidentally introduced to Tasmania and then mainland Australia, where it began decimating forests of this highly susceptible tree species. Nematodes were identified attacking *S. noctilio* in New Zealand and researchers demonstrated that these extraordinary nematodes have dimorphic females that can either live as free-living mycetophages or as parasites of *S. noctilio* (Bedding and Akhurst, 1974). This nematode has been widely introduced throughout pine plantations in Australia. Infested logs are inoculated with nematodes, which then search for and infect host larvae. Infected larvae continue development and the adult females subsequently emerging are sterile but disseminate nematodes during attempted oviposition. The presence of mycetophagous forms of this nematode facilitates mass production as well as multiplication and persistence in the field, independent of *S. noctilio* populations. Levels of nematode parasitism in *S. noctilio* of close to 100% have been reported and this nematode is now generally recognized as the main controlling agent of *S. noctilio* in Australia (Bedding, 1993). Activity of this nematode is economically very beneficial because when the nematode is not present, this pest has been shown to cause up to 80% tree mortality, resulting in potential losses of A$1–4 billion in each 30 year rotation (Bedding, 1993).

Inundative augmentative releases

The principal applications of pathogens for control of arthropods have been inundative augmentative releases as microbial pesticides. This type of application strategy is most often used with pathogens that can be efficiently mass-produced and have a broader host range. Worldwide, there are many species of microorganisms in use or being developed for inundative microbial control (Lacey and Goettel, 1995; Shah and Goettel, 1999). We will briefly describe several examples of successful microbial control pesticides.

Bacillus thuringiensis

The bacterium *Bacillus thuringiensis* is by far the most successful entomopathogen used as a microbial control agent to date. Thousands of tons of this bacterium are applied annually throughout the world to control lepidopteran, coleopteran and dipteran pests in terrestrial and aquatic habitats. It is a spore-forming bacterium that produces a crystalline parasporal body at sporulation (Tanada and Kaya, 1993). After ingestion, the parasporal bodies are dissolved and toxins are activated in the midgut. The activated proteins bind to specific receptor sites, resulting in lysis of midgut cells and subsequent death of the host. There are over 50 serotypes of *B. thuringiensis* producing an array of crystal proteins specific to different insects. Even though parasporal bodies dissolve in the guts of many insects, toxicity is expressed only if specific binding sites are present on the midgut cells. This makes different serovars very host specific. For instance, *B. thuringiensis* var. *israelensis* is toxic only to certain dipterous insects such as mosquito and blackfly larvae, while *B. thuringiensis* var. *kurstaki* is toxic only to certain Lepidoptera.

Steinernema *spp.*

Numerous commercial microbial insecticides are based on several species of steinernematid nematodes. These are used against an array of soil-dwelling insects and some steinernematids are very host specific. These nematodes gain entry into the host through the mouth, anus or even sometimes through the body wall. Upon entry into the host, the nematode releases a symbiotic bacterium, which in turn rapidly colonizes and kills the host (Gaugler and Kaya, 1990). These nematodes are important because they can actively search for or ambush hosts living in cryptic habitats, e.g. usually soil, and it is generally difficult to control pests in such microhabitats.

Beauveria bassiana

Beauveria bassiana is a common fungal pathogen of insects that can be found worldwide. It has been a focus for commercial production for the last 20–30 years and has been used to control the Colorado potato beetle in the former USSR since the mid-1960s and pine caterpillars in China since the mid-1970s. More recently it has been registered in several European, North American and South American countries for control of a wide array of pests, ranging from the European corn borer to greenhouse thrips (Shah and Goettel, 1999). *B. bassiana* conidia can be mass produced in bi-phasic fermentation systems and can be stored dry at room temperature for over a year (Feng *et al.*, 1994; Jaronski and Goettel, 1997). The conidia penetrate the host cuticle after landing on the host and germinating. Mycelia then ramify within the host haemocoel, eventually killing the host. Upon host death, and under conditions of high humidity, the fungus sporulates on the cadaver surface. Conidia are persistent in the soil but short-lived on leaf surfaces exposed to sunlight.

Non-target effects of pest control using entomopathogens

Ecological effects of microbial control agents on non-target organisms can come about either through direct infection of the non-target organisms or through indirect effects, namely depletion of the target population. In essence, these effects are essentially the same as those arising with the use of any biological control agent, be it microbial or arthropod. When evaluating the risk posed by microbial control agents, whether they are applied inundatively or in the classical sense, it is important to include in the risk analysis the alternatives to not controlling the pest, i.e. the devastation to non-target organisms caused by depletion of food resources, competition with aggressive pests or effects of the use of broad spectrum chemical treatments.

As with arthropod biological control agents, direct effects on mortality of non-target organisms can be predicted from the agent's ecological host range, i.e. the range of species infected in the field. Difficulties in predicting the ecological host range are discussed below. Infection of non-target secondary hosts has been previously suggested as being beneficial to biological control efforts, serving to provide a reservoir of inoculum and thus promoting later infections in target host populations (Fargues and Remaudière, 1978). Although this may be beneficial as far as control of the target host is concerned, the degree of harm that such secondary infections would pose to non-target populations needs to be considered. Today direct infection of any non-target host is usually considered an undesirable effect in any biological control programme.

Pathogens rarely directly infect parasitoids within a host. However, they often outcompete parasitoids within the host tissue, resulting in death of the immature parasitoid within its infected host (Flexner *et al.*, 1986; Goettel *et al.*, 1990). Such an outcome must be viewed as competitive displacement rather than direct pathogenicity of non-target hosts. Other than causing direct mortality of non-target organisms or competitive displacement of parasitoids, pathogens can also cause sublethal effects, which could also have an important direct effect. For instance, some sublethal effects of entomopathogens include reduced food consumption, longevity and fecundity. Unfortunately, very little is known about potential sublethal effects of entomopathogens and only recently has this subject received attention.

In addition to direct effects of pathogens on target and potentially non-target arthropods, there can be indirect effects due to depletion of the target host population which in turn influences non-target arthropods either directly associated with the pest, e.g. predators and parasitoids, or non-targets indirectly associated but impacted by presence of the pest. In many instances, pest problems occur with exotic pests or pests in manipulated ecosystems and, in such instances, one must view any potential indirect non-target effects with perspective about the already disturbed state of these systems. Although indirect non-target effects are, of course, much more difficult to predict or document than direct effects, they are essentially the same for use of pathogens as for use of arthropods in biological control.

Classical biological control

Classical biological control introductions are aimed at permanent establishment of the natural enemy in pest populations. The majority of classical biological control releases of pathogens have involved their use against introduced pests with which they evolved, with few examples of the use of new associations (exotic natural enemies released against native pests or pests not occurring in the area of origin of the natural enemy). Classical biological control requires serious evaluation of potential non-target effects before release of the natural enemy. Researchers must hypothesize regarding non-target effects of released agents in the new area based on laboratory studies, literature reviews and studies of non-target effects in the area of origin. It must be remembered that, although establishment of the natural enemy would be permanent, levels of the pathogen in the environment will probably be highly associated with the principal host, i.e. only at high levels during epizootics and then present in the microhabitats inhabited by the principal host (Maddox *et al.*, 1992).

When an exotic pathogen becomes established and provides long-term control, as would be expected in classical control, this is permanent. Ecological effects may be minimal if the target population is introduced in the first place and the natural enemy is highly host specific. However, pathogen introductions may be very undesirable if endemic target invertebrates are affected. For instance, in arguments against the use of new associations, using the example of the introduction of the Australian fungal pathogen *Entomophaga grylli* (pathotype 3) for control of North American grasshoppers (which are all considered to be indigenous), Lockwood (1993) speculated that such introductions could produce adverse effects such as competitive suppression or extinction of both native biological control agents and non-target acridids. Such suppression might in turn result in loss of biodiversity, proliferation of weeds, proliferation of previously innocuous acridid species, disruption of plant community structure, suppression of essential organisms vectored by grasshoppers, and disruption of food chains and other cycling processes. In rebuttal, Carruthers and Onsager (1993) pointed out that new associations have been used successfully in the past without causing serious environmental problems. They believed that Lockwood (1993) overstated the potential negative impacts of use of the new association approach for classical control of grasshoppers and that he devoted substantial discussion to hypothetical adverse impacts. Although they admitted that none of the undesirable scenarios hypothesized by Lockwood (1993) could be categorically deemed as an impossibility, they argued that such catastrophic events would be highly improbable. They contended that it is unrealistic to assume that all species of grasshoppers are potential hosts to the introduced fungus and they provided results of laboratory tests that demonstrated a limited host range, even within Acrididae. Since there are more than 300 grasshopper species present in North America, they contend that the probability is infinitesimal that organisms that rely on grasshoppers would be catastrophically deprived of grasshoppers. Furthermore, there is no data to support Lockwood's hypothesis regarding destruction of current weed suppression mechanisms, major restructuring of plant communities, annihilation of vertebrate parasites, or disruption of food chains or nutrient cycles. Despite the many hypothetical scenarios surrounding results of the introduction of *E. grylli* pathotype 3 into North America, current evidence suggests that the frequency of infection has declined to levels such that long-term survival of this pathotype in North America is questionable (Bidochka *et al.*, 1996).

To date there is no evidence of detrimental ecological effects from deliberate introductions of entomopathogens for use in 'classical' biological control. However, insights of possible detrimental effects can be obtained from studying natural epizootics of indigenous strains. For instance, Ullyett and Schonken (1940) reported that although an epizootic of the entomopathogenic fungus, *Z. radicans* (as *Entomophthora shaerosperma*) in a lepidopteran pest in South Africa produced a profound immediate reduction of the pest during environmental weather conditions favourable to the pathogen, the activity of the pathogen was ultimately responsible for an increase in the average density of the pest 12 weeks later. There are theoretical grounds to speculate that natural epizootics in lepidopteran populations which are already under regulation by insect parasitoids can cause host populations to cycle with greater amplitude and longer periods (Myers, 1993; Berryman, 1996). The basis of the theory is that virulent, obligate pathogens (such as nuclear polyhedrosis viruses) kill a large proportion of the host population, which then temporarily discouples the parasitoid–prey interaction. Furthermore, it is proposed that environmental conditions that favour invertebrate pests are not necessarily those that favour the microbial pathogen, whereas environmental conditions that favour invertebrate pests also generally favour their invertebrate parasitoids and predators. Consequently, the overall hypothesis is that pathogens may sometimes be responsible for the cyclical nature of insect outbreaks (although see Bowers *et al.* (1993), whose models demonstrate that cycles would not be caused by pathogens alone). Based on this theory, Valenti (1998) questions the long-term benefits of the recent decimation of gypsy moth populations by the fungus *E. maimaiga*. However, *E. maimaiga* differs from viruses upon which this theory is based because, after epizootics, a detectable host population is usually present and *E. maimaiga* continues to be found causing infections in subsequent years, i.e. the crash in the host population is not so absolute. Only time will tell if the fungus will continue to hold gypsy moth populations in check or ‘exacerbate a century old problem’ by disrupting the population dynamics of this introduced pest. Certainly the present population crash is viewed as a great benefit by foresters and homeowners on the eastern seaboard of North America.

Much has been written regarding criteria for choosing parasitoids and predators for introduction. It has been suggested that at present we have too few examples of successful classical biological control using pathogens to identify criteria for selection. In opposition to general opinions that virulent pathogens should be introduced, some researchers have proposed that pathogens that are weakly virulent can be highly successful for introduction to suppress exotic pests over the long term (Anderson and May, 1980). Furthermore, little consideration has been given to pathogens that debilitate rather than kill the host (e.g. microsporidia). Such weaker pathogens possibly might not induce cycling of outbreaks (Ewald, 1987) although there is clearly a need for studies more closely investigating the combinations of factors that generate cycles in the field. On the other hand, would it be deleterious to introduce a more virulent natural enemy providing control that causes cycling if the outbreak peaks after crashes were widely spaced and not extreme? In fact, many pathogens are neither highly virulent nor very weak. Perhaps at present one of the best indicators that a pathogen should be considered for classical biological control would be its ability to decrease host populations in its endemic area. In addition, it is evident that a thorough knowledge of all natural enemies associated with a host (both pathogens and arthropod predators and parasitoids) would be optimal before introductions are planned. We strongly suggest that planning for biological control programmes should be holistic, with consideration of both pathogens and arthropod natural enemies.

Inundative augmentative releases

There has always been primary concern regarding direct effects of microbial pesticides on non-target organisms and this is reflected in regulations and registration requirements. These pathogens must be applied inundatively to provide adequate control because they are either nonexistent in the area of application or because existing levels are inadequate. Consequently, immediately after application, dose levels are usually higher than would normally occur in nature. Factors that potentially could directly affect non-target organisms are: (i) endemnicity of the pathogen; (ii) dose; (iii) host range; (iv) persistence; and (v) dispersal. Because non-indigenous pathogens have the potential to become established, risks to non-targets could be similar to those in classical control (see previous section). Even with indigenous pathogens, consideration must still be given to the potential risks of introduction of new strains or pathotypes having different attributes from the indigenous strains. With very specific indigenous entomopathogens, there is usually little concern over direct impacts on non-target organisms. However, for the most part, pathogens developed as microbial insecticides to date include in their host range more than just the target host. Consequently, direct impacts on non-target invertebrates closely related to the target host are common with pathogens having more than one host species. Even though entomopathogens used inundatively may directly affect non-target organisms, there is no evidence to suggest that these pathogens become established in populations of non-targets, thereby causing long-term effects.

Even detrimental effects can sometimes provide longer-term advantages. For instance, large-scale applications of *B. thuringiensis* var. *kurstaki* against the gypsy moth in eastern West Virginia were found to affect the richness and abundance of native, non-target Lepidoptera in the short term (Sample *et al.*, 1996). However, these authors predicted that, in the long term, the effects of reduced abundance of the target host resulting from the *B. thuringiensis* var. *kurstaki* application may be beneficial for some of the native species, due to reduced competition from *L. dispar.*

In addition to effects caused by target host depletion, other unexpected indirect effects can result from inundative use of indigenous entomopathogens. For instance, Weseloh *et al.* (1983) attributed higher populations of a braconid parasitoid in *B. thuringiensis* treated areas to a sublethal effect on the target host, *L. dispar.* They suggested that the bacterium retarded development of the host, thereby providing the parasitoid with a longer oviposition period, which resulted in a larger proportion of larvae being parasitized. This example, although seemingly beneficial in this instance, illustrates the need for long-term ecological studies. Even though there are numerous possible direct and indirect effects of microbial pesticides on non-target organisms, in the end it must be realized that it is generally not possible to manipulate one part of the ecosystem (i.e. the pest population) without in some way affecting other components (i.e. non-target organisms). With microbial pesticides, most detrimental effects are usually reversible, as pathogen levels eventually return to background levels following application. Therefore, if detrimental effects are noted, a decision could be made to alter or discontinue the application of the microbial control agent and the situation should eventually return to the pre-application state.

A special case: genetically engineered pathogens

Genetically altered microorganisms provide a special challenge because they have never previously existed in the environment in their altered state. Potential risks to non-targets and to the environment include transfer of genetic material to other microbes, intentional or inadvertent expansion of host range, irreversible depletion of the target host (which can also be considered a goal) and competitive displacement of the endemic parent strain. Possible direct effects are easier to predict and much information can be gained by comparison of the altered organism with the attributes of the parent strain. Predictions can also be made based on the exact nature of the introduced trait. Indirect effects may be more difficult to predict. However, once again much will depend on the organism itself and on the introduced trait. As with classical control, irreversible effects could occur if a genetically altered organism with detrimental non-target effects were to become established. In essence, many issues regarding release of a genetically engineered pathogen are similar to those that need to be considered before introduction of a pathogen for classical control, because release can be permanent.

Methods for evaluating non-target effects

Some of the main reasons for reluctance to use entomopathogens in biological control have been our lack of knowledge regarding their taxonomy, host specificity and ecology, as well as which characteristics should be used to select the most appropriate agent. Regarding non-target effects, protocols and methods for evaluation of the potential risks of introductions of entomopathogens are lacking. As discussed above, non-target considerations differ for different types of biological control using pathogens. To date, few biological control programmes using microorganisms have included a comprehensive field evaluation of direct and indirect non-target effects. The reader is referred to Hajek and Goettel (2000) for a broad overview of methods for evaluating the effects of entomopathogens on non-targets. Below, we discuss the difficulties inherent in using laboratory-generated data to predict non-target effects in the field.

While all evaluations of non-target effects should include a controlled laboratory study, the applicability of these results to field situations is questionable (Maddox *et al.*, 1992; Goettel, 1994, 1995). Numerous observational studies suggest that many hosts infected by pathogens in the laboratory are never found infected in the field (Maddox *et al.*, 1992; Hajek and Butler, 2000). These observations have been substantiated by comparing laboratory host specificity of the lepidopteran specific fungal pathogen *E. maimaiga* (Hajek *et al.*, 1995a) with infections among non-target Lepidoptera collected during epizootics caused by *E. maimaiga* in *L. dispar* populations in the field (Hajek *et al.*, 1996). Laboratory studies using optimal conditions for infection suggested that this pathogen might infect quite a few different species, but at low levels. During field studies, only two individuals out of 1511 lepidopteran larvae collected and reared were infected with *E. maimaiga*. Because the two individuals infected belonged to common species, total infection levels were only 0.3% (*Malacosoma disstria*) and 1.0% (*Catocala ilia*). Evaluating the 20 species that were bioassayed in the laboratory as well as collected in the field during the epizootic, six species became infected in the laboratory while only one of these was infected in the field, and at a much lower level than in the laboratory. These results demonstrated that laboratory host range was much more diverse than the host range found in the field and percentage infection was higher in the laboratory. This raises questions about the reliance only on data from laboratory studies in order to predict whether non-target species will be infected in the field.

Goettel (1995) argues that little useful information is to be gained from extensive laboratory non-target organism testing for indigenous pathogens that are to be used inundatively; such testing does not necessarily provide an indication of safety of the organism in question and inundative application of an indigenous pathogen is in essence no different from using a synthetic chemical insecticide, although pathogens are generally more specific and do not cause the side effects characteristic of synthetic chemical insecticides, e.g. residues. Only through close monitoring of effects in the field during operational use would actual detrimental effects be detected; such studies are needed to improve our understanding of host specificity under field conditions. In contrast, with genetically engineered organisms and pathogens contemplated for introduction for classical control, we must largely rely on laboratory-generated data, since host range cannot truly be determined until release in the field. We now know, however, that in many cases laboratory host range is much broader than that expected to occur in the field. This discrepancy between laboratory and field host range suggests that future laboratory evaluations should attempt to mimic as much as possible the parameters that are to be expected in the field. If possible, such studies should be followed by semi-field studies or field studies in the area of origin of the agent to add to data from laboratory host range evaluations (Hajek and Goettel, 2000). It may still be possible to use pathogens that are highly pathogenic to certain non-target organisms in situations where exposure of the non-targets to the pathogen is prevented or limited. In such situations, detailed knowledge of pathogen persistence (both in space and time) and dispersal will be crucial.

Conclusions

Pathogens remain one of the greatest untapped resources for pest management. They offer a great potential for biological control, both for inundative application and for classical releases. As with any pest control tactic, there is no doubt that using microorganisms for management of pest arthropods poses potential risks to non-target organisms. However, these effects can be avoided or minimized through careful choice of agents. Risks must also be weighed against the detrimental effects of the pest organism itself or of alternative methods employed for its management. A better understanding of factors determining host specificity as well as basic pathogen and target host ecology and epidemiology is needed to better predict potential detrimental effects. Long-term studies of entomopathogens already registered and in use could be used as model systems for risk assessment. As new field diagnostic methods are being developed, it is becoming possible to economically monitor and evaluate effects of pathogens under field conditions. Increasing knowledge of pathogen taxonomy, biology and epizootiology should allow for more useful and more precise risk assessments in the future. Past experiences have demonstrated that pathogens can be used effectively and safely with minimal effects on non-target organisms. Compared with chemical insecticides, they offer a better and much safer alternative for use in integrated pest management systems.

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6

Insect Biological Control and Non-target Effects: a European Perspective

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Abstract

A 4-year research project on 'Evaluating Environmental Risks of Biocontrol Introductions in Europe' (ERBIC) is described, and early results are presented. The project focuses on arthropod biological control (using both microbial and macrobial agents), and uses literature review, case studies with empirical work and various types of modelling to illuminate risk to non-target organisms. These methods will hopefully lead to the development of usable methodologies and guidelines for risk assessment in arthropod biological control, by the project's completion in 2002.

Reviewing existing published and unpublished data on the classical biological control of insects (a first step in this project) has revealed that for only 1.5% of introductions is there some data regarding the realized field

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specificity of the agent. For a tiny proportion of introductions there are quantitative data regarding mortality in non-targets. From these cases, with some extrapolation, we can deduce that 10% or less of classical biological control introductions in the past led to population changes in non-targets. Data on population-level effects from simulated uses or trials suggest that 49% of inundative or augmentative uses of agents led to (local, short-term) population changes for non-targets.

Case studies into: (i) exotic specialist parasitoids used in the greenhouse; (ii) exotic generalist parasitoids used inundatively in the field; (iii) exotic generalist predators used inundatively; and (iv) fungi and nematodes used as bioinsecticides, are outlined. The results so far demonstrate: (i) the apparent safety of *Trichogramma* (generalist parasitoid) releases in Switzerland, despite rare species within its host range; (ii) the lack of overwintering capability in northern Italy in one generalist predator (*Orius insidiosis*), but its presence in another (*Harmonia axyridis*); (iii) little evidence that the predation of certain stages of native predators by introduced predators will enhance environmental risks in the cases in question; and (iv) the apparent safety of bioinsecticide releases of particular pathogen strains for important naturally occurring predators when exposed directly or by feeding on infected prey.

Introduction: the ERBIC project

In 1998, a 4-year research project on ‘Evaluating Environmental Risks of Biological Control Introductions into Europe’ (ERBIC) began, funded by the European Union (EU). The overall aim is to facilitate the development of sustainable, biologically based, agricultural production systems, in line with the commitments of many EU governments to reduce the use of chemical pesticides. This may be achievable with biological control, where this is both a practicable and environmentally benign solution to pest-management problems. In this context, the ERBIC project has two major roles. The first is to review and examine current and past biological control practices against arthropods to assess their environmental impact. The second is to develop appropriate methodologies and guidelines to allow the assessment of biological control agents of arthropod and practices in the future.

A three-pronged approach is being used to achieve these aims. Firstly, a review of the known non-target effects of arthropod biological control worldwide was conducted. Secondly, four European biological control systems, in different agroecosystems, were taken as case studies, and subjected to various empirical investigations. Thirdly, ecological theory is being used as a conceptual basis for considering non-target risk, in an attempt to unify these case studies within a broader framework. Here we discuss in detail the results of the review of worldwide knowledge of arthropod biological control, followed by a brief overview of the empirical and modelling work.

Several reviews already address the issue of non-target impacts in biological control (e.g. Howarth, 1983, 1991; Pimentel *et al.*, 1984; Samways, 1994; Lockwood, 1996; Simberloff and Stiling, 1996; Stiling and Simberloff, 1999). Earlier papers raised questions regarding specific biological control introductions, and brought up many conceptual issues regarding the potential complexity of such effects (e.g. Howarth, 1983; 1991). More recent papers, such as Stiling and Simberloff (1999), begin to tackle the problem in a much more quantitative manner. However, there is still a need for further quantitative analysis, for the bringing together of a more exhaustive list of examples, and in general to go further beyond the anecdotal. Most would agree that the examples discussed in Howarth (1991), Simberloff and Stiling (1996) and other similar papers, while they highlight the potential pitfalls of biological control and the potential complexity of non-target effects in practice, do not provide enough information to address the following questions:

1. Does the (arthropod) biological control community now have a correct and consistent implementation strategy, in terms of balancing risk and benefit?
2. Have risk assessment and host range testing procedures in arthropod biological control improved significantly over the course of time?
3. Do we know enough about non-target effects to solve these questions already?
4. What research do we need to do? What can we learn further from the historical record of arthropod biological control?

In addition, many of the examples given in the literature are to some extent circumstantial, in that the causality of various recorded population reductions and extinctions is unclear. Thus, some authors lay the blame on biological control in cases where the causes of extinction have been unclear, while others argue that the lack or weakness of evidence exonerates biological control (Simberloff and Stiling, 1996). It seems that a more objective look at the frequency of recorded non-target effects is necessary. Stiling and Simberloff (1999) do indeed go some way towards this, and a further effort is presented here, specifically directed at arthropod biological control.

What this process may reveal in the end is how little we actually do know. Thus, it may be very difficult, at this stage, to make the comparisons on common ground with other pest control measures that are necessary for policy decisions. Perhaps we do not have the information to damn, or bless, biological control but, more importantly, to think in these terms is simplistic and impractical. What we really need are data that enable us to ensure that biological control is done responsibly in the future, and allow us to demonstrate convincingly that this is being achieved. Therefore, any information that illuminates current and previous methodology, and thus allows us to think critically about the best ways of using natural enemies in an environmentally benign fashion, is useful. Only to a limited extent do these data exist, so this review is both a first step and a justification of the ERBIC project.

A retrospective analysis of published and unpublished data

Methods

Published and unpublished sources for this review were found by several means. These included conventional literature search, consulting staff at CABI *Bioscience*, UK, and those from the ERBIC project, and direct correspondence with 30 other experts in biological control worldwide (see Acknowledgements). By using such methods, we should have uncovered all, or nearly all, observations of non-target effects generated by introductions against arthropods that exist so far.

Data relating to introductions of insects, microbial agents and nematodes, which attack arthropod pests, were collected. Both classical introductions and other types of biological control (augmentation/inundation) were considered, to allow us to draw comparisons between different strategies. The data were organized into records in which target/agent/non-target combinations at a particular place (country) were defined. These records have a number of other fields, giving more details. Many of these correspond to fields in BIOCAT, the database of classical biological control introductions of insects (Greathead and Greathead, 1992). Apart from such BIOCAT fields, which give general data on the introduction and its success, there are fields describing the name of the non-target, its classification (order, family), and the literature reference from which the non-target effect originated. Other fields are: (i) biological control type (classical or inundation/augmentation); (ii) agent type (parasitoid, fungus, nematode, insect predator); and (iii) study type (RR = recorded rearing, M = study of mortality or parasitism, PR = study of population reduction, E = extinction). The nature of the non-target effect itself is summarized in a few sentences in one field, and this is translated into a severity index (0–9) in another. This allows further semi-quantitative analysis. The severity index is shown in Table 6.1. This index is somewhat arbitrary, but allows the various forms of non-target impact (mortality, population reduction and extinction) to be assessed in a comparative manner. Only if mortality was above a certain level was this assumed to cause a population-level effect. Thus, a severity index of three can mean either a recorded mortality level greater than 40% or evidence of a minor population-level impact. Hawkins *et al.* (1993) and Hawkins and Cornell (1994) show that where the maximum parasitoid-induced mortality in a target is less than

Table 6.1. Suggested severity indices for non-target effects of biological control.

0	No records of consumption, infection, parasitism, population suppression or extinction
1	< 5% mortality induced by consumption/infection/parasitism or equivalent in sublethal effects on fecundity, with no recorded significant population consequences
2	5–40% mortality from consumption/infection/parasitism, with no recorded significant population consequences
3	> 40% mortality from consumption/infection/parasitism (at one time on a local population) and/or significant (> 10%) short-term depression of a local population
4	> 40% short-term depression of a local population, or permanent significant (> 10%) depression of a local population
5	> 40% long-term suppression of a local population, or > 10% long-term suppression of a global population ('global' meaning an area of 100 × 100 km or more)
6	> 40% long-term suppression of a global population
7	Apparent local extinction, or extinction where recolonization likely in the long term
8	Certified local extinction where recolonization is unlikely or impossible (due to an island habitat and/or limited species range, so could imply extinction of the species)
9	Certified extinction over an area of 100 × 100 km or more

30% in classical biological control, severe suppression and resulting successful control are unlikely. In most cases, a mortality level of at least 40% appears necessary to lead to a serious population-level impact, and it seems likely that similar principles apply to non-target effects.

The field of 'study type' deserves some elaboration. Some studies are simply records of hosts (collected in the field) from which a parasitoid has been reared (recorded rearing, RR). Others record parasitism or other forms of mortality by percentage (mortality, M). Some studies actually measure the reductions of populations observed at some spatial scale over some time scale (population reduction, PR). A small number of reports consider suspected extinctions or extirpations (extinction, E). Each type of study has a different range of effects that it can detect. For example, studies that only examine mortality cannot determine population-level impacts. For some studies, the effect looked for may not have been found, but the presence of more minor effects is neither ruled out nor proven. This would produce a 'zero' in terms of the severity index recorded, but such a zero does not itself imply any impact at all. More generally, where non-target effects of a given level were suspected and looked for, but none were found, these 'zeros' have been included in the database, as they may provide some useful information. However, studies were most often undertaken when non-target impacts were suspected. This implies that the frequency of such 'non-effects' cannot be used as an estimate of the proportion of biological control attempts not leading to non-target effects of a given level. Only unbiased data, collected for another reason, or intended to be exhaustive studies of a region, can be used to gain this type of insight (e.g. Funasaki *et al.*, 1988; Hawkins and Marino, 1997).

Results

Overview of the extent and nature of the evidence

In total, 428 records (target/non-target/agent/location) were gathered, comprising both classical introductions and other agent uses. Of the 5279 classical introductions of insects against insects listed in BIOCAT, 80 (i.e. 1.5%) had one or more such non-target effect records associated with it. These 80 introductions had over four non-target effect records each, on average, such that there were 379 records (target/non-target/agent/location) relating to such classical introductions. Of these, 365 (i.e. 96.3%) had a non-zero severity level (i.e. some effect or host use was detected). The majority of these records are simple rearing records, or quantified records of mortality.

By contrast, the evidence for population reduction or extinction is often fairly weak or circumstantial, and for many such reports a 'severity = zero' has been recorded. This does not imply that we can say for sure that there was no effect. Rather, it follows from our intention for the database to be a collection of the evidence rather than of speculation. This should not be viewed as an attempt to exonerate biological control. In terms of the severity index, the majority of records actually gathered for classical biological control fall below 3, which implies no recorded population impact and a maximum recorded mortality rate of less than 40%. Only 14 of the introductions recorded in BIOCAT have a study associated with them that gives a non-target effect record with a severity index of 3 or greater. These are listed in Table 6.2. This low number, combined with the low proportion of introductions investigated at all, goes to show how little actual evidence we have for, or against, the general existence and severity of these effects.

The rest of the database is composed of inundative or augmentative uses of agents. We do not make a distinction between augmentation and inundation here. Many of these examples involve the use of nematodes, usually Steinernematids or Heterorhabditids. Studies of inundation or augmentation usually involve simulated biological control application on plots or microcosms in which non-targets are sampled, rather than studies during or after actual operational use. It is assumed that these studies give accurate data about the non-target effects of these biological control methods in practice. Thirty-five non-target effect records were gained from publications on inundation. However, since soil-dwelling organisms were

Table 6.2. Classical biological control introductions of insects associated with a non-target effect with a severity index (see Table 6.1) of 3 or greater.

Agent	Target(s)	Year	Location	Non-target(s)	Severity	Reference
Microtonus aethiopoides	*Sitona discoides, Listronotus bonariensis*	1982	New Zealand	*Irenimus aemulator, Irenimus aequalis, Nonnotus aibicans*	3	Barratt *et al.*, 1997
Chilocorus nigritus	*Aspidiotus destructor*	1939	Mauritus/Africa	*Chilocorus wahlbergi*	5	Samways, 1989
Cryptolaemus montrouzieri	*Planococcus kenyae, Planococcus fragilis*	1929	Kenya	*Dactylopius opuntiae*	3	Goeden and Louda, 1976
Cryptolaemus montrouzieri	*Dysmicoccus brevipes*	1938	Mauritius	*Dactylopius opuntiae*	3	Goeden and Louda, 1976
Copidosoma floridanum	*Chrysodeixis eriosoma*	1969	New Zealand	'Trichogrammatoidea'	5	Roberts, 1986
Bessa remota	*Levuana iridescens*	1925	Fiji	*Heteropan dolens*	7	Tothill *et al.*, 1930
Cotesia flavipes	*Diatraea saccharalis, Diatraea lineolata*	1984	Mexico	*Apanteles diatraea*	6	Bennett, 1993
Trichopoda pilipes	*Nezara viridula*	1962	Hawaii	*Coleotichus blackburniae*	3	Follet *et al.*, 1999
Trissolcus basalis	*Nezara viridula*	1962	Hawaii	*Coleotichus blackburniae*	3	Follet *et al.*, 1999
Cotesia flavipes	*Diatraea saccharalis*	1971	Brazil	*Metagonistylum minese, Paratheresia claripalpis*	6	Bennett, 1993
Aphytis holoxanthus	*Chrysomphalus aonidum*	1960	USA	*Pseudhomalopoda prima*	6	Bennett, 1993
Aphytis holoxanthus	*Chrysomphalus aonidum*	1962	Brazil	*Aphytis costalimai*	6	Bennett, 1993
Compsilura concinnata	*Lymantria dispar, Nygmia phaeorrhoea*	1906	USA	*Cecropia* spp.	3	Stiling and Simberloff, 1999
Trigonospila brevifacies	*Epiphyas postvittana*	1967	New Zealand	*Xanthopimpla rhopalocerus*	5	Roberts, 1986; Russell, 1986

often grouped into broad classes in these studies, this figure is an underestimate of the number of non-target impacts *per se*. In general, the potential host range of the agents was known, from laboratory studies, to be very large, but dependent on dose and conditions. The field host range, however, was usually undetermined. In most cases, only the population consequences were measured, as mortality not leading to a population consequence was of less interest to the investigators. Factors such as persistence and dispersal processes, which might determine the environmental impact in practice, were given greater emphasis.

Classical biological control: 1. Studies of rearing records, parasitism and mortality rates

Classical and inundative/augmentative biological control were considered separately when looking for general patterns of severity. In classical biological control, studies which either looked simply for rearing records or percentage parasitism levels found most evidence for only minor utilization of the non-target host or prey species (Fig. 6.1a). Restricting ourselves to quantitative studies does not fundamentally change this pattern (Fig. 6.1b). These data suggest that many agents utilize non-target hosts at a low level, and do not generate sufficient mortality to imply some kind of population-level effect. Stiling and Simberloff (1999) used studies of proportion success in classical biological control to argue that 10–26% of cases where a non-target is within the agent's fundamental host range result in population-level impacts. The current data suggest this may be an overestimate, implying that the true proportion is 8% or less.

Classical biological control: 2. Studies of population-level impacts and extinctions

These studies form a small proportion of the effects recorded, but they do show that there are a substantial number of apparently serious population-level effects that stand up to scrutiny (Fig. 6.2). The choice of 'study systems' is, of course, biased; many of these examples effectively selected themselves, when population-level effects were noticed. However, even here there are occasional cases where initial suspicions of an effect at a population level were found to be unsubstantiated. When they were detected, most of the effects could be classified into severity categories 5 and 6, implying > 40% population level impacts at a local or global scale. This shows either that quite severe effects are more likely than more minor ones, or that more severe non-target suppression is necessary for the effect to be noticed. The latter explanation implies that minor population impacts are much more frequent than they appear to be.

Turning to extinction, there have been questions raised about the role of biological control in species depletion in island ecosystems, but little evidence singling it out as an overriding cause in particular cases. For example, a few local entomologists argue that the early history of biological

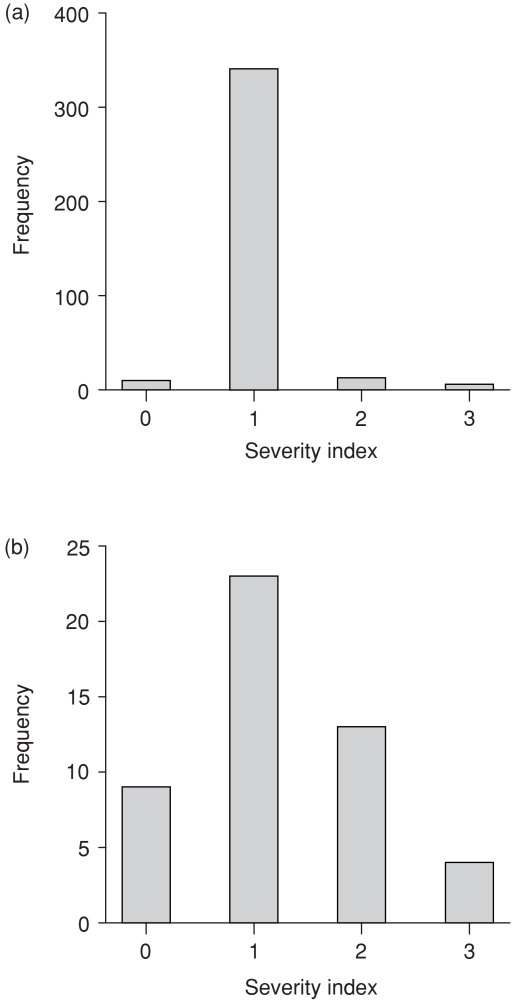

Fig. 6.1. Frequencies of non-target effects from studies of parasitism or rearing records in classical biological control, as classified according to the severity index (Table 6.1): 0, mortality or parasitism looked for, but none found; 1, rearing record of unspecified proportions, or quantified mortality < 5%; 2, mortality of 5–40%; 3, mortality > 40%. (a) All records (RR and M studies); (b) only records of quantified mortality (M studies).

control had a substantial impact on the native Hawaiian fauna (Zimmerman, 1948, 1958; Howarth, 1985). However, proving that particular cases of extinction were the fault of biological control, or even that biological control was a major contributory factor, is now almost impossible. There is one relatively clear example for Fiji, however. This is the local extinction of the native moth *Heteropan dolens*, following the introduction of the parasitoid *Bessa remota* against the levuana moth *Levuana iridescens*, in 1925 (Tothill *et al.*, 1930; Howarth, 1985; Roberts, 1986). It seems unlikely that this was an isolated incident amongst the island ecosystems where biological control took place at that time.

There is even less evidence for the role of biological control introductions in insect extinction in the post-DDT era. Biological control is implicated as a possible contributory factor in the extinction of *Murgantia histronica*, which occurred following two biological control introductions into Hawaii in 1962 (Howarth, 1991). However, a recent review of this case (Follet *et al.*, 1999) suggests that the evidence is essentially circumstantial. Furthermore, *M. histronica* was considered a pest itself, and its role as a potential host of one of the agents used was well known. A more recent example of a possible extinction is that of the displacement of the native parasitoid, *Apanteles diatraeae*, by the introduced parasitoid, *Cotesia flavipes*, on the sugarcane borer, *Diatraea saccharalis*. The native parasitoid could no longer be collected from the sugarcane borer in 1984–1985, implying severe population reduction and possible extinction (Bennett, 1993). Such cases of displacement are difficult to interpret, however. Firstly, extinction *per se* was not shown (for example, the natural habitat and native hosts were not examined). Secondly, a native species that maintains itself only by

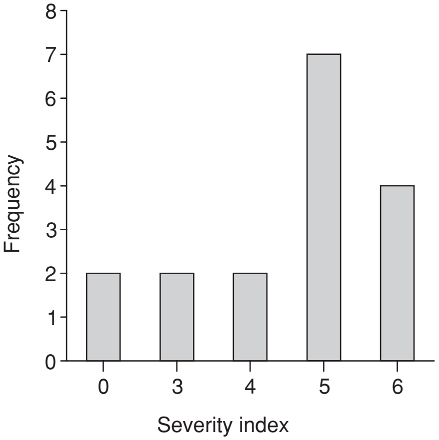

Fig. 6.2. Frequencies of non-target effects from studies of population reduction, classified according to the severity index (Table 6.1): 0, no solid evidence of population-level effects due to biological control; 3, significant (> 10%) local, short-term, population depression; 4, > 40% short-term depression, or > 10% long-term depression of a local population; 5, > 40% long-term suppression of a local population- or > 10% suppression of a global population; 6, > 40% long-term suppression of a global population.

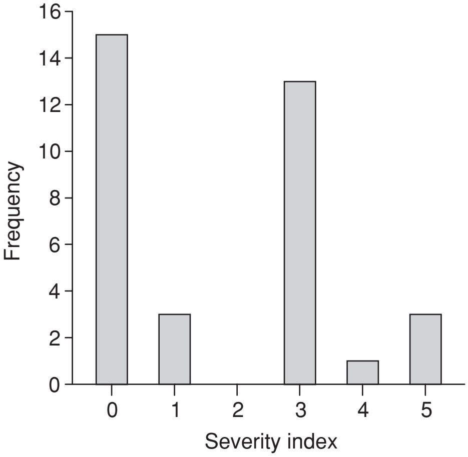

Fig. 6.3. Severity index (see Table 6.1) in studies of augmentation or inundation, including both studies measuring mortality rates and those measuring population-level effects.

parasitizing a pest on an agricultural crop could be said to be 'living on borrowed time' in any case. So, extinction in a natural habitat is perhaps more meaningful (but less likely to be detected).

We can conclude that very little is known for sure about the extinction of insects caused by biological control introductions. During the early 20th century these probably occurred on a number of occasions on island habitats, but by now the passage of time, the presence of other factors and lack of detailed investigation makes it difficult to pin down the causes in many individual cases. From 1960 onwards, while there are the 'borderline cases' above, there seems to be little evidence for extinction caused principally by insect introductions. However, this lack of evidence may tell us very little, and is best not interpreted as a reason for complacency.

Severity in augmentation and inundation

These studies, which mainly examine population reduction (in field trials or simulated scenarios), form a less biased body of data. Many of the agents are generalists, but their use is considered sufficiently safe due to their relative lack of persistence, and the consequent transience (or simply nonexistence) of their non-target impact. As field tests of pure host range are rare, the number of cases of severity level 1 are greatly under-represented (Fig. 6.3). The large number of zeros appears from studies where (local) population effects have been looked for and none found. It appears that many releases are in this sense safe. There are a substantial number of low intensity population level impacts (index = 3) and a few more serious ones, however. In fact, it seems that about 8.5% of monitored non-target species that may have been affected by inundation/augmentation suffered quite serious local population effects (severity index 5 or above). Almost half (49%) suffered some kind of population-level impact, or equivalent mortality (compared with ≤ 8% for classical biological control).

Patterns over time in classical biological control

The number of classical biological control introductions against insects increased from the late 19th century to mid-20th century (Fig. 6.4). This was followed by a sustained period of high activity from the 1950s to the 1970s (see also Greathead and Greathead, 1992). The proportion of these introductions leading to recorded non-target effects was very much higher at the beginning of biological control history, and has tended to fall ever since (Fig. 6.4b). Limiting ourselves to those with a severity index greater than 2, this pattern disappears, and two temporal clumps of non-target effect records are revealed (Fig. 6.4c). Perhaps this pattern is due to the idiosyncrasies of the records involved (there are relatively few of these). Alternatively, the more recent clump may have been caused by increased monitoring for such effects in recent years, while the earlier records reflect a greater prevalence of such effects.

Biological control success and non-target effects

An attempt was made to see if the number of recorded non-target effects could be related to the success category (see Fig. 6.5) of classical biological control (as stored in BIOCAT). The results are shown as proportions of introductions leading to effects of a given severity (> 0 and > 2, giving Fig. 6.5a and b, respectively). Few non-target effects have been noted where

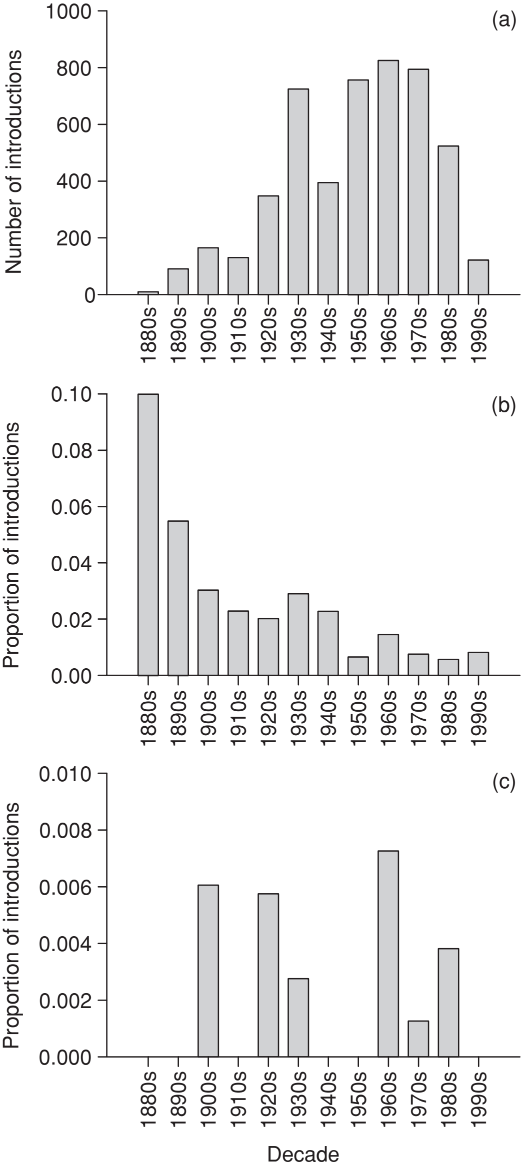

Fig. 6.4. Patterns of non-target effects over time. (a) Number of classical introductions of arthropod control agents per decade, as recorded in BIOCAT; (b) proportions of introductions for each decade leading to a recorded non-target effect of any level; (c) proportions of introductions for each decade leading to recorded non-target effects of severity index > 2 (see Table 6.1).

the outcome of the introduction itself was not ascertained, which is not surprising. There are a substantial number of non-target effects for introductions where agents did not seem to establish on the target pest (Fig. 6.5a). This implies that some control agents have established as persisting populations on non-targets, and thus are likely to have a population-level impact. There is little direct evidence of these impacts themselves, however (Fig. 6.5b).

Looking at all impacts (Fig. 6.5a), we see that a relatively large proportion of cases where agents have established on the target, but have not led even to a partial biological control success, have been recorded as inducing non-target effects (Fig. 6.5a). These are mainly minor impacts (compare Fig. 6.5a with Fig. 6.5b). We can think of three potential explanations. The first assumes that the host range of an agent is not correlated with its biological control success. Thus, the realized host ranges of agents in these

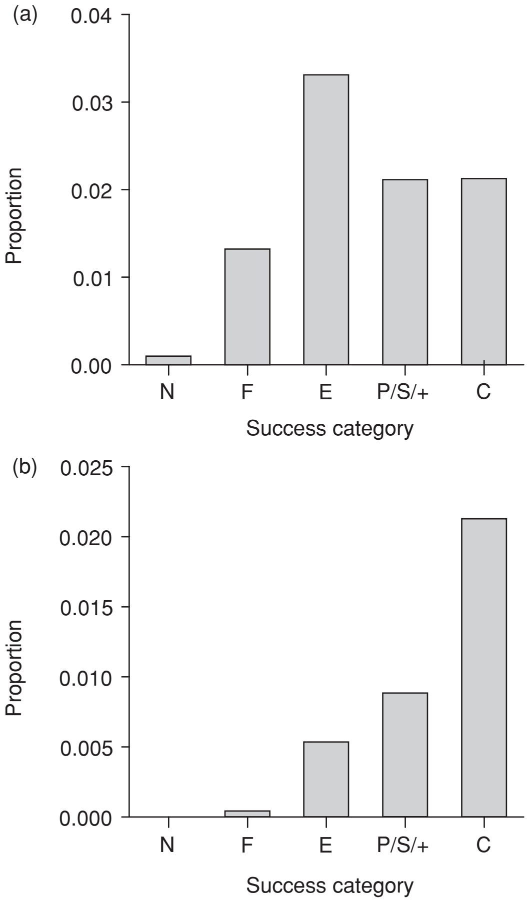

Fig. 6.5. Classical biological control success and non-target effects. (a) Success category (in BIOCAT) and proportion with a recorded non-target effect of any level. Actual data (success category, introductions with effects, total introductions in parentheses): N, 1 (1015); F, 32 (2419); E, 31 (937); P/S/+, 12 (567); C, 3 (141). (b) Success category and proportion with a recorded non-target effect of severity > 2 (see Table 6.1). Actual data: N, 0 (1015); F, 1 (2419); E, 5 (937); P/S/+, 5 (567); C, 3 (141). Success categories are defined as follows: N, unknown; F, agent failed to establish; E, agent established, but no recorded suppression of target (or other indicators of success); P/S/+, partial control, substantial control, or substantial or complete control in combination with another agent; C, complete control. See also Greathead and Greathead (1992).

different success brackets will be equal. The extra proportion of records in the 'established only' class must therefore be a result of sampling bias. This bias could have been caused by the extra likelihood of looking for agents on non-targets when the agent is not abundant after release. More exhaustive post-release studies are not usually conducted where the agent is abundant and effective, but often are carried out after less successful releases. Alternatively, realized host range may be correlated in some way with the success of the agent, in that polyphagous agents may be more likely to simply establish and have little effect on the target (but may be recorded feeding on non-targets). The third explanation is that both the non-target records and the relative lack of biological control success have the same root cause: some kind of inadequacy in the care with which biological control was carried out; in particular, agent choice. Poor agent choice may mean both poor effectiveness and poor host range testing, and such examples are likely to lead to more cases in the 'established only' column.

Limiting ourselves to more severe non-target effects, we see a different pattern. It seems as if successful biological control introductions have a greater proportion of their potential non-target effects (i.e. species attacked at all in the field) realized as major ones (> 40% mortality, population-level impacts) (compare Fig. 6.5a and b). Of course, there may be a sampling bias behind this relationship too, or it may simply be down to chance (given the very small sample size of 14). Alternatively, ecological theory (or theories) can be used as a basis to make testable predictions about such a relationship. There are several complex arguments that could be invoked for this, but these will not be presented here. For now, we simply note that such arguments lead to two possible predictions. These are that intermediate successes have the greatest proportion of non-target effects, or that the more successful introductions are more likely to lead to non-target effects. There is clearly more evidence for the latter relationship, but as there are a number of possible explanations for this, this does little to narrow down the mechanisms involved. In addition, the amalgamation of some success classes in Fig. 6.5b makes the relationship seem clearer than the raw data suggest, and the very low sample size implies that we should not read too much into this relationship.

Database conclusions

Overall, this attempt at an exhaustive data search has underlined our ignorance of the degree to which non-target effects occur. Only 1.5% of classical biological control introductions against insects appear to have associated with them any data on the realized host specificity of the agent and the existence of non-target effects at any level. These data do give us some information, but by virtue of their selectivity and the fact that they address only a small number of cases (which have not been chosen randomly), they cannot inform us as to the extent of the problem. In the face of such ignorance, our only option is to take the problem seriously.

The semi-quantitative study of mortality induced in non-targets has shown that minor non-target effects outnumber the major effects. Thus, only 8% of the instances of non-target mortality seem serious, in the sense that they may lead to population-level effects. However, as 62.6% of releases have involved polyphagous species, attacking an average of about two non-target hosts each (Stiling and Simberloff, 1999), perhaps 10% of introductions have had serious population consequences. We can therefore guess that about 530 non-targets have been affected at a population level over the history of biological control. This history, however, is not static with respect to the strategy of those making the releases. Different individuals and organizations over the course of over a century have had different practices, in the context of prevailing attitudes to the environment that have changed radically. The proportion of introductions recorded to cause non-target effects has decreased tenfold over the course of this history.

Inundative and augmentative methods rarely have post-release investigations either, but here we have assumed that field or microcosm trials give a realistic impression of the non-target effects generated by these methods. This is not necessarily the case, as the use of exotic generalists may result in their establishment in new areas, which might lead to a range of environmental consequences that such trials cannot anticipate. This is another area of ignorance. What we do know about inundative methods is not particularly reassuring: 49% of these seem to have some population consequences for local fauna, and 8% produce > 40% population reductions. Their use may be justified by the transience and locality of the impacts, particularly in agroecosystems distant from truly natural habitats (or with agents that disperse little). However, it is important that the ecological basis for the transience of any effects, and the conditions that prohibit exotic agents from establishing permanently, are well understood in all application scenarios. Otherwise, the safety of these methods is merely an assertion. The case studies below address these issues, among others.

Case studies in European biological control

Here we briefly introduce the case study systems used in the ERBIC project, and report on the general nature of non-target risks in these systems, experimental plans and some early results. Differing projects with different demands have progressed to different extents, hence the heterogeneity in the presentation of results. The systems are methods of (mainly exotic) agent use in inundative or glasshouse introductions. These are either established methods or methods in development, which may become common practice in the future. The studies so far completed have addressed the risk issues in the systems concerned, such as host range, overwintering ability and dispersal processes. As the project proceeds, the studies will develop to consider more ecological aspects of the risks, and feature parametrization of models used to address ecological questions, such as the outcome of competitive exclusion.

Case 1: exotic specialist parasitoids

Every year, billions of exotic beneficial organisms, such as parasitoids in the genus *Encarsia*, are produced and released in greenhouses to control the tobacco whitefly, *Bemisia tabaci*, and the greenhouse whitefly, *Trialeurodes vaporariorum*. Such exotic parasitoid species may interact and compete with native parasitoids that may spontaneously enter the greenhouse. Exotic parasitoids may also leave the greenhouse, attack native whiteflies in the field, and thus compete with native parasitoid species. Although the *Encarsia* species used in biological control of whitefly pests are specific to the Aleyrodidae, most have a broad host range of species and genera within this family. Thus, they may directly or indirectly interact with other *Encarsia* species, other endoparasitoids (*Amitus*, *Cales*, *Euderomphale*), or primary ecto-endoparasitoids (*Eretmocerus*), by utilizing the same whitefly species in the field. Exotic whitefly–parasitoid systems in greenhouses have been studied for over 25 years, resulting in the development of both reliable and sustainable biological methods for the control of whitefly pests (van Lenteren and Martin, 1999). However, little is yet known about the ecology and host range of *Encarsia formosa* in natural ecosystems (Loomans and van Lenteren, 1999). This system is therefore particularly appropriate for studying the effects of introduced agents on competition among parasitoids, on both native and alien host (whitefly) species in different climatic regions. This study also allows us to test the hypothesis that exotic parasitoids originating from tropical areas cannot survive under temperate field conditions, and therefore form only a temporary environmental hazard. The effects of idiosyncratic life history strategies of *Encarsia* species, such as facultative hyperparasitism, on competition, can also be examined.

The impact of mass-releases of exotic parasitoids on the native insect fauna is currently being evaluated in field studies in The Netherlands, and this work will also be repeated later in Italy. There are several key tasks:

- surveying the whitefly and parasitoid populations in Europe;
- developing reliable identification tools, based on traditional and molecular methods;
- life-table studies to analyse demographic impacts;
- host selection and host specificity studies, to determine the range of target and non-target hosts attacked;

- studies on interspecific competition in different climatic zones (mediterranean and temperate), and the delineation of food webs, with particular emphasis on heteronomous hyperparasitoids;
- studies on the dispersal process, to assess the degree to which *Encarsia* migrate from the target crop to natural habitats in different circumstances;
- studies of physical requirements of exotic introduced beneficials, particularly in relation to overwintering.

The native and exotic whitefly fauna and their introduced and native parasitoids were first surveyed in natural habitats and private gardens in various parts of The Netherlands, concentrating on areas surrounding release sites. So far, 15 species of whiteflies are known in The Netherlands, and about 65 in the western Palaearctic region generally. More than 45 species of whitefly parasitoids are known in the western Palaearctic. In The Netherlands, we have collected data on two native species, *Encarsia tricolor* and *Euderomphale chelidonii*, parasitizing the native whitefly species *Aleyrodes proletella* (on cabbage cultivars) and *Aleyrodes lonicerae* (on blackberry), in the outdoors, from July to October. The exotic *E. formosa* was collected outdoors on the greenhouse whitefly, *Trialeurodes vaporariorum* (on melon) as well as on native whitefly species (*A. proletella* on cabbage and *Chelidonium lonicerae*; *A. lonicerae* on blackberry and strawberry). They were found in private gardens and natural settings in the neighbourhood of greenhouse complexes (but more than 500 m from the nearest greenhouse).

Transect trap experiments were performed from September 1999 onwards in order to study the magnitude and direction of dispersal of a release of 70,000 *E. formosa* in a 1.8 ha tomato greenhouse. *Encarsia* dispersal was monitored using yellow sticky traps and trap plants (Brussels sprouts infested with the native whitefly species *A. proletella*) in the four main wind directions from the release, and by surveying plants infested with whiteflies in the surrounding area. The greenhouse whitefly was found up to 3 km from the nearest glasshouse, and *E. formosa* up to 500 m from the release site.

Overwintering studies with *E. formosa* and native species (*E. tricolor*) were set up using both native and exotic host species. These hosts were parasitized in the laboratory and then exposed to natural conditions for the winter period, to see how many survived. Finally, to evaluate the host range and the impact of hyperparasitoids, both field and laboratory experiments are being carried out. These examine the interactions among primary exotic parasitoids (*E. formosa*), facultative exotic hyperparasitoids (*Encarsia pergandiella*) and native parasitoids (*E. tricolor*). They mainly focus on behavioural interactions, competition processes among parasitoids and host specificity.

Case 2: exotic generalist parasitoids

Generalist *Trichogramma* parasitoids are released in very large numbers against a range of crop pests. Because most of these are polyphagous, they may affect many non-target host species. However, different *Trichogramma* species have different host ranges and, particularly, habitat preferences, which influence their exact impact on non-targets. This case study deals in particular with inundative mass-releases of *Trichogramma brassicae* in Switzerland, carried out annually to control the European corn borer (*Ostrinia nubilalis*) in maize. Adult parasitoids may disperse into natural habitats and attack a range of butterflies, including endangered species. Furthermore, the released *T. brassicae* may interact with native parasitoids and thereby displace them. This system is therefore particularly appropriate for field studies examining the effects of an exotic generalist parasitoid on populations of pests and non-target species, and as a case study for modelling this issue. Using this system, we can try to test the hypothesis that (under certain conditions) exotic generalist parasitoids can be safely used for inundative releases. Our approaches include detailed investigations into overwintering, dispersal, host range and competition.

Overwintering studies with *T. brassicae* were set up with eight different hosts between the end of September and the end of October 1998. The study revealed that this egg parasitoid is able to overwinter (north of the Alps) on several hosts, despite the fact that the winter 1998/1999 was harsher than usual, with temperatures dropping to –10 or –20°C on several days. In addition, extensive monitoring was carried out to check whether introduced exotic *T. brassicae* could be found in the surroundings of release sites in the following year. In fact, *T. brassicae* and two endemic *Trichogramma* species were found during the whole season, including prior to commercial releases. Thus, we are sure that *T. brassicae* can and do overwinter in Switzerland.

Again, in this case study, knowledge of the dispersal capacity of the agent is essential for risk assessment. A field experiment examining this was designed to match the conditions of commercial releases. Two maize fields of about 1 ha each were selected and 100,000 adults of *T. brassicae* released in each. Dispersal was monitored through parasitism of *O. nubilalis* egg masses. Since previous investigations indicated a high dispersal potential of *T. brassicae*, egg masses were exposed at ten locations between the maize field and 1 km distance in the four main directions. The results indicated very limited dispersal from maize fields. Only in one case were parasitized eggs found more than 12 m from the edge of the maize field. In another experiment, we investigated dispersal behaviour within a meadow. About 40,000 *T. brassicae* adults were released from a point source and dispersal was measured with transparent sticky traps, installed up to 32 m from the release point. After three days, the density function obtained did not show any decrease in numbers with distance from the release point (within the experimental area). This indicates that many parasitoids had left this 32 m radius circle already.

The specificity of *T. brassicae* for hosts was also investigated. Eighteen species within all major families of butterflies (half of which were named on the red list for endangered species), and six moth species, were tested. Most of these species were readily accepted by *T. brassicae* females, resulting in a high rate of parasitism and emergence of parasitoids. However, eggs of several butterfly species were weakly or not at all accepted, although they have previously been shown to be suitable hosts for *T. brassicae*. For a few species, eggs were accepted, but no parasitoid offspring emerged. Several field or semi-field experiments were carried out to further elucidate the risk of parasitism to non-targets under more natural conditions. These have shown that low parasitism rates are experienced by eggs of non-targets when exposed on their respective host plants in a meadow. We then tested whether the degree of parasitism by *T. brassicae* of the same host eggs depended on whether the eggs were found in maize crops or in meadows. The meadow is the actual habitat of the endangered butterflies in question. We found that parasitism was dramatically reduced in meadows compared with maize.

In order to evaluate the potential for competition between *T. brassicae* and native parasitoids, we singled out the native larval parasitoid *Lydella thompsoni* (Dipt.: Tachinidae) for study. This tachinid is the most abundant and efficient native European corn borer parasitoid within the study area. European corn borer larvae experience a mean parasitism rate of about 20% from *L. thompsoni*. In the spring generation, *L. thompsoni* also parasitizes native hosts in natural habitats, migrating into maize fields for subsequent generations on the European corn borer in early summer. It is possible that *T. brassicae* may overflow from their release sites in the summer to neighbouring habitats, and parasitize native hosts of *L. thompsoni* during their ovipositional period. The effect of this on populations of such native hosts may have impacts on the abundance of *L. thompsoni*, as it relies on these hosts in spring. Therefore, we investigated whether *T. brassicae* attacks potential spring hosts of the indigenous tachinid, in both the laboratory and the field. By far the most abundant host species were found to be *Archanara geminipuncta* (Lep.: Noctuidae) and *Chilo phragmitellus* (Lep.: Pyralidae), both feeding on common reed (*Phragmites australis*) (although *C. phragmitellus* has not been found parasitized by the tachinid in the present study so far). If freshly laid eggs of *A. geminipuncta* were detached from the stalks and offered to *T. brassicae* in the laboratory, 80% of the females parasitized these eggs. In contrast, naturally laid eggs, as they are hidden underneath the leaf sheaths of common reed stalks, were virtually free of parasitism. Naturally laid egg masses of *C. phragmitellus* are similar to the egg masses of the European corn borer, and were accepted under laboratory conditions, although less than 33% of the egg masses were parasitized. Examination in the field of egg masses of both native host species in common reed sites near release areas did not reveal any sign of parasitism.

In conclusion, our study indicates that *T. brassicae* can successfully overwinter in Switzerland. Many non-target butterflies, including endangered species, can be attacked by *T. brassicae*, but low parasitism rates in field cage and field experiments in meadows indicate that the risks are relatively minor. Finally, populations of the indigenous tachinid *L. thompsoni* do not appear to be at risk, since its most important spring hosts were not found parasitized by *T. brassicae*.

Case 3: generalist exotic predators

Exotic and endemic predatory bugs in the genus *Orius*, and ladybird beetles such as *Harmonia axyridis* and *Adalia bipunctata* are being released in the fields and greenhouses of Europe for the control of thrips, aphids and other small insects and mites. These predators, however, are generalists, attacking most animals that they encounter which are small enough to handle. The exotic species *Orius insidiosus*, for example, was introduced and released on a large scale in Europe before a proper inventory was made of native species, such as *Orius laevigatus*, which might be able to control thrips. Thus, the exotic species may be able to establish and compete with native predators in the field for the same prey species. This introduction is therefore a suitable case study of how an exotic generalist predator may establish and compete with related, endemic species. Such a system can be used to test the hypothesis that generalist predators which are strongly related to endemic species should not be released before the role of these native predators has been evaluated. The exotic generalist coccinellid predator *H. axyridis* provides an analogous example, and so is an additional case study. Investigations that are being conducted in Italy have so far focused on overwintering ability, establishment of agents in natural habitats, intra-guild predation (predation between species on the same trophic level) and cannibalism.

Orius insidiosus

Over the past few years, *O. insidiosus* has been released in several places in Italy. Field surveys have been carried out to look for the establishment of *O. insidiosus* on several vegetable and ornamental crops around sites of release. No evidence of establishment has been recorded up to now. This result was confirmed by overwintering experiments, which were carried out in Sicily and Cesena, Italy. These indicated that the exotic *O. insidiosus* cannot overwinter in northern Italy, and is very unlikely to do so even in southern Italy. Laboratory experiments were carried out on intra-guild predation and cannibalism in *O. insidiosus* (exotic) and *O. laevigatus* (native) species, to assess the nature of their likely interactions in the field. These experiments examined many combinations of numbers and instars of the two species, and their prey, in confined areas, with a high degree of replication (30 times). The numbers of different contacts occurring between the individuals, as well as predation or cannibalism events, were recorded over 2 h. These preliminary experiments indicated a low propensity for cannibalism and/or intra-guild predation in both the native *O. laevigatus* and the exotic *O. insidiosus*. Nevertheless, when no food is available, there is an increase in cannibalism and intra-guild predation.

Harmonia axyridis

First results indicated that *H. axyridis* is able to successfully overwinter in northern Italy. In order to confirm these data, recorded in 1998–1999, a semi-field trial has been established by placing rearing cages under an outdoor shelter, in Bologna (northern Italy). The native species *A. bipunctata* and *Propylaea quatuordecimpunctata* are being used as controls. Laboratory experiments have been carried out, examining cannibalism and intra-guild predation of eggs by adult females and fourth instar larvae of exotic and native ladybird beetles. The experiments examined:

- cannibalism in the exotic *H. axyridis* and in the native species (i.e. *A. bipunctata*; *A. variegata*; *P. quatuordecimpunctata*);
- intra-guild predation: exotic versus native species eggs (i.e. *H. axyridis* vs. *A. bipunctata* eggs; *H. axyridis* vs. *A. variegata* eggs; *H. axyridis* vs. *P. quatuordecimpunctata* eggs);
- intra-guild predation: native versus exotic species eggs (i.e. *A. bipunctata* vs. *H. axyridis* eggs; *A. variegata* vs. *H. axyridis* eggs; *P. quatuordecimpunctata* vs. *H. axyridis* eggs).

There was significantly lower intra-guild predation by *H. axyridis* of eggs of the native species *A. bipunctata* than cannibalism by *H. axyridis* of its own eggs. No significant difference was detected between the degree of intra-guild egg predation by *H. axyridis* of the native species (*P. quatuordecimpunctata*, *A. bipunctata* and *A. variegata*) and cannibalism by these species on their own eggs. For all the coccinellid species, the level of cannibalism or egg predation was higher in the experiments without aphids.

These results indicate that the exotic species *H. axyridis* does not demonstrate intra-guild predation of native species at a level intrinsically higher than that of the cannibalism native species experience on their own. In addition, when aphids are present, these more usual (and perhaps preferred) prey lead to a great reduction in rates of cannibalism and intra-guild predation. It is thus concluded that *H. axyridis* does show a high potential for cannibalism and a high aphid predation rate, but there is little evidence to suggest that this species would have a large negative impact on native species by direct means such as intra-guild predation.

Case 4: fungi and nematodes as bioinsecticides

Generalist exotic and endemic microbial biological control agents in the form of fungi (*Metarhizium* and *Beauveria*) and nematodes (*Steinernema*) are mass-released for the control of pests in many fields and greenhouses in Europe. Non-target effects on beneficial insects (predators, parasitoids, bumble bees), endangered butterflies and soil-dwelling detritivores (springtails) have seldom, and then only superficially, been studied. Long-term studies on the ecosystem-level effects of these releases have never been undertaken. The critical factors believed to determine the potential for these releases to cause non-target impacts include virulence ('host range'), persistence and dispersal. Research on these factors is being carried out in Finland, using turnip rapeseed as the model agroecosystem. This cropping system has a well-studied key pest, the pollen beetle (*Meligethes aeneus*, Col.: Nitidulidae). Much is also known about its natural enemy complex, which includes important non-target 'beneficials'. In order to obtain background information on the role of pathogens as mortality factors of non-target organisms in this system, some 35 species and over 5000 individuals of Carabidae, Coccinellidae, Staphylinidae, Collembola and spiders have been collected and processed. The results show that natural occurrence of entomopathogenic fungi and nematodes in the adults of the chosen arthropod groups occurring in turnip rape fields is rare, as only a few individuals have been found infected (0.2%), mainly by *Beauveria bassiana*.

The susceptibility of generalist predators to entomopathogenic fungi has been examined in the laboratory, mainly using two isolates of the Deutromycete *Metarhizium anisopliae*. Two routes of exposure to the pathogen have been investigated, ingestion of infected prey and pick-up via fungal propagules applied to soil. No *Pterostichus melarius* (Col.: Carabidae) died due to fungal infection after having been fed with larvae of *M. aeneus* infected by *M. anisopliae* ($n = 60$). Thus, it appears that spraying the crop with spores (of the selected isolates) does not pose a risk to *P. melarius* via its feeding on larvae that drop from the crop to the soil. None of the tested individuals ($n = 60$) of four selected carabid species (*P. melarius, Pterostichus niger*, *Carabus granulatus* and *Harpalus rufipes*) exposed to fungal-treated sand died of fungal infection. Thus, these two isolates of *M. anisopliae* appear to be safe to these carabids when used as soil treatments in turnip rape seed fields. However, a partly plant-feeding carabid species, *Amara eurynota*, was somewhat susceptible to these two isolates of *M. anisopliae* and one isolate of *B. bassiana*. Furthermore, *A. eurynota* was susceptible to *M. anisopliae* by both infection methods. The virulence of these two isolates of *M. anisopliae*, however, is significantly lower to *A. eurynota* than to the larvae of the target pest, *M. aeneus*. Based on our previous studies, there is reason to believe that adults of the pollen beetle can be latently infected by entomopathogenic fungi, and thereby disperse the pathogens over the long distances between the target and surrounding non-target habitats. However, of a total of 1489 field-collected individuals, only 175 (i.e. 12%) yielded fungi during incubation. None of these was *M. anisopliae* or *B. bassiana.* Hence latent infections by these fungi in populations of overwintering beetles are rare. The situation may be different, however, if the spore densities in the field soils are artificially augmented.

Thus, this research has so far demonstrated:

- the low rate of natural occurrence of entomopathogenic fungi and nematodes in the target agroecosystems;
- the safety of releases for important naturally occurring generalist predators feeding on target prey infected with entomopathogenic fungi;
- the safety of releases for important naturally occurring predators directly exposed to candidate entomopathogenic fungi myco-insecticides;
- the potential for entomopathogens to disperse long distances via latent infections of the host or non-target species.

Mathematical modelling and ecological theory

The ERBIC project also features the linking of theoretical ecology and mathematical modelling with the issue of non-target effects generally, and the case studies above in particular. The use of these techniques will extend from the use of ecological concepts for problem definition to the construction of stage-structured models to address more quantitative questions in specific systems. When considering non-target effects, it is important that an ecologically enlightened view of the nature of these effects is taken, and also of existing ecological theory. This process of applying theory has revealed both unanticipated application of existing theory, and ‘gaps’ where more theoretical work would be helpful to address the applied problems we face. Thus, this process is both intrinsically useful and gives pointers as to where further empirical and theoretical work is needed.

The use of the case studies above to provide examples as the focus for further modelling is the next step. Some of these systems form more idiosyncratic versions of general ecological problems. For example, assessing the effects of exotic heteronomous hyperparasitoids on native parasitoid species forms an example of competitive displacement, as does the case of interacting native and exotic coccinellids. Simple models can encompass both systems, but more complex models are needed to highlight the distinctions between these systems, and the unique factors they feature which affect non-target risk (such as intra-guild predation and facultative hyperparasitism). Coupled with the collection of relevant empirical data, gathered with specific modelling approaches in mind, a very powerful understanding of risk factors in these case studies can be developed. The added generality of the simpler models ensures that this understanding goes beyond the confines of the systems examined.

While the later process, relating modelling and case studies, is in its early stages, some progress has been made with the more general modelling. The first modelling exercise has focused on transient impacts in classical biological control, especially on the factors determining the minimum densities of non-target species. Factors leading to a large risk of non-target extinction via transient agent levels in classical introductions are: (i) high density of the host which is to be controlled; (ii) high conversion efficiency of these hosts into parasitoids; (iii) high dispersal rates of agents into the non-target habitats; and (iv) high searching efficiencies of the agent for the non-target in its native habitat.

Where the searching efficiency of the agent for the target is very high, the non-target could suffer quite a large transient impact, despite being the much less preferred and/or much less easily found host (Lynch and Ives, 1999). This is because it is the level of the absolute searching efficiency for the non-target that matters, rather than that measured relative to the searching efficiency for the target. Some details of the population dynamics of the non-target influence the minimum non-target density, but do so in a relatively subtle way. For example, high population growth rates and/or scramble competition in the non-target reduce the extinction risk subtly. Searching efficiency for the non-target assessed under choice (target host present) or non-choice (target host absent) conditions may be appropriate for predicting the severity of non-target effects. This is because less preferred hosts, not usually chosen in choice tests, can still be at a large risk in practice due to changing host acceptance behaviour in scenarios where density of the preferred host is low (i.e. non-choice situations). Which experimental conditions are more relevant to predicting the severity of the impact in practice depends on the exact nature of the local dynamics of the target–agent interaction. As these details may be quite difficult to predict in advance, non-choice searching efficiencies may have to be used to give predictions about non-target impact which err on the side of caution. Thus, this type of modelling exercise can focus empirical work in assessing risks, so that what we know in advance about an introduction is maximized under conditions of limited time and resources. However, it also delineates the ultimate limits of what can easily be known in advance.

Overview

Reviewing the current evidence regarding non-target effects in insect biological control has revealed the full extent of our ignorance. There is a clear need for post-release studies of classical biological control, both for releases carried out in the future, and for retrospective studies. The data we currently have are sampled from the set of all introductions in a way that is somewhat biased. Effects have been looked for where they were likely to be found, or have been discovered by accident. Due to this bias, we have little data on which to base estimates of probabilities of various effects (i.e. the risks). What we do know suggests that 10% or less of the biological control introductions carried out to date have one or more population-level non-target effects associated with them.

As for inundative and augmentative methods, the literature review revealed that such methods seem to lead to population-level non-target effects quite often, but that these releases are justified by their transience and boundedness in space. The processes generating these effects, and the ecological validity of these justifications for agent use, are the subject of empirical investigation in the ERBIC case studies. Thus, these experiments first tackle issues such as dispersal and aspects of host range (virulence in pathogens, and acceptance or suitability in parasitoids). They also tackle factors affecting the establishment of exotic agents, such as overwintering potential, thus addressing issues of spatial boundedness, and the persistence of non-target effects.

The processes by which population impacts actually occur (in both classical and inundative biological control) are also the subjects of detailed study. These are ecological in nature, and include population impacts caused directly by parasitism or infection, and via competitive processes. Tackling these issues can be aided by ecological theory, including modelling, at various levels of quantification and sophistication. As well as making quantitative predictions, modelling helps to integrate the examination of different systems, and allows mechanistic approaches in cases where fewer data are available. Thus, we may shed some light on factors affecting risk in classical biological control, despite the fact that the data are sparse.

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7

Biological Control in Africa and its Possible Effects on Biodiversity

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Abstract

Biological control efforts in tropical Africa have been most often directed at invading exotic species and are conducted in rapidly changing landscapes, in which the flora, fauna and ecological interactions are imperfectly known. Faced with major threats to food production and ecosystem destruction, biological control practitioners have been obliged to take a pragmatic approach to minimize the risks of undesirable ecological effects. Workshops convened under the auspices of the Inter-African Phytosanitary Council and the FAO brought together local stakeholders and international agencies to develop the various projects on classical biological control. Procedures required as pre-conditions for the importation of biological control agents have usually involved third country quarantine and host specificity tests, which – following the FAO code of conduct – have become more rigorous in recent years. Thus far, extensive pre-release testing of candidate control agents for the ability to attack native relatives of target species has not usually been required. Post-release documentation of impact has often included detailed ecological studies, but these have focused largely on agricultural habitats. The procedures followed and insights gained in relation to indirect effects are discussed in the light of classical biological control campaigns involving parasitoids and predators against exotic Homoptera, tetranychid mites, lepidopterous stemborers, thrips, the larger grain borer and water hyacinth, and the inundative use of fungal pathogens against grasshoppers.

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Introduction

In the 1970s, biological control was considered an important, though marginal, specialist discipline in agriculture. The ‘safety’ of the organisms used rested largely on the professionalism and sense of responsibility of the individual practitioners. Based on previous ecologically disastrous experiences, the use of vertebrates and molluscs was generally avoided, but specific or stenophagous insect parasitoids and predators were thought to be absolutely safe. In summary, the reputation of classical biological control, from an ecological perspective, was that of a ‘knight in shining armour’, who could do no wrong.

At about the time that we were celebrating the centenary of the vedalia beetle releases in California and the success of 100 years of biological control worldwide, reports began to emerge from Hawaii of biological control agents allegedly playing a role in the disappearance of native species. Some 14% of the 243 biological control agents released in Hawaii had attacked non-target, native or beneficial species (review in Howarth, 1991). None of the agents released from 1969 onward had been recorded as feeding on desirable species and, indeed, Howarth’s favoured example of extinction through non-target effects of biological control, the case of *Levuana iridescens* Bethune-Baker (Lepidoptera, Zygaenidae), subsequently proved unable to stand up to scrutiny (Sands, 1997). Nevertheless, the knight’s armour was beginning to look a little tarnished by the attacks.

With the United Nations Conference on the Environment and Development, held in Rio de Janeiro in 1992, practitioners of biological control received both encouragement and criticism. On the one hand, the Rio conference recognized integrated pest management, based on biological control, as a key element in reversing agriculture’s hazardous dependence on pesticides and establishing a more environmentally friendly paradigm. On the other hand, conservationists were also encouraged to review the threats to biodiversity in general and they came to see biological control as constituting such a threat. The previously impeccable environmental and social credentials of biological control thus came under attack from an unexpected quarter.

The publication of the FAO Code of Conduct for the Import and Release of Exotic Biological Control Agents in 1996 (FAO, 1996) tried to codify the steps in the introduction of biological control agents in line with the requests from the environmental movement. In fact, for most practitioners of biological control, the FAO code of conduct simply endorsed the good practice previously employed. It is at this level of ‘environmental sensitivity’ that we are currently executing biological control in Africa.

In the meantime, however, environmental activists have raised the expectations for biological control still further by demanding that screening of candidate control agents should ensure that they pose no threat of untoward effects on native flora and fauna. In Europe and North America, where undisturbed or little-disturbed land represents only a small fraction of the total area (sometimes less than 10%, if forests, mostly managed, are excluded), the sentiment that its fauna and flora could be threatened is understandable. Moreover, the species in these islands of undisturbed land, often nature reserves and national parks, are relatively well known, which gives a name, a face, to the possible victims – and facilitates the process of identifying possible threats. The great majority of people in these countries are not involved in agriculture (2% in agriculture is a common figure); they are well educated and often sensitive to environmental issues (though not perhaps as knowledgeable as one would like); and, most importantly, they are usually affluent. In sum, they are ready and able to 'pay a little more' to ensure that agriculture does not endanger what little remains of natural diversity.

In total contrast, in Africa the great majority of the population (often around 80%) tends to be involved in agriculture; many are poorly educated (in many countries the majority cannot read or write); and overwhelmingly they are poor (with a large proportion living below the United Nations poverty line of US$1 per day). If people are aware of environmental hazards, they often regard them as unavoidable, and conservation of biodiversity is a distant abstraction, when the business of daily survival presents many more pressing concerns. Though statistics are difficult to obtain, the pattern of land use is evidently quite different from that in Europe. In many regions, land under active cultivation comprises 10% or less of the total, while in others practically all land is always under cultivation of some sort (Thenkabail, 1999). In-field biodiversity (Vandermeer *et al.*, 1998) is higher than in Europe or North America and plot size is generally small. Undisturbed areas with statutory protection (national parks and reserves) also usually constitute a small proportion (though often more than in European countries). The greater part of the land area is in an intermediate and changing state, consisting of natural fallow regrowth, or semi-natural vegetation which is exploited for grazing, hunting, gathering firewood or extraction of timber. Only a fraction of the biodiversity of the natural areas has been documented, while the various impacts on biodiversity involved in the intermediate forms of exploitation are scarcely understood at all. Though overall human population densities are often low, the rate of population growth (and associated loss of natural habitats) is generally high, indicating the urgency of the need to understand biodiversity in order to protect it effectively.

One impact on biodiversity is, however, very evident: increased food production in Africa, in response to a growing population and other pressures, has largely been coming from an expansion of the area under cultivation, rather than intensified production within existing farmland. It is this clearing of natural, or semi-natural, vegetation that represents the overwhelming threat to biodiversity in Africa. In this context, farmers are most likely to respond to an invading pest, disease or weed that reduces crop yields by attempting to increase the area under cultivation. Economically, people have few alternatives.

It is immediately evident that the governments and peoples of Africa have rather different priorities from those of their counterparts in Europe. Their overwhelming concern is to feed, and raise the living standards of, an ever-growing population. The Consultative Group for International Agricultural Research (CGIAR), of which the International Institute of Tropical Agriculture (IITA) is one of the founding members, is responding to this need. IITA's mission statement says that:

> IITA aims to enhance the food security, income and well-being of resource-poor people primarily in the humid and sub-humid zones of sub-Saharan Africa by conducting research and related activities to increase agricultural production, improve food systems, and sustainably manage natural resources, in partnership with national and international stakeholders.

The emphasis thus is on sustainable productivity increase, which is only possible by protecting the environment for the use of future generations. It should be noted that today the issue of sustainability is accorded the same level of priority as 'productivity'.

Preservation of biodiversity is one of the focus areas of the CGIAR, not because the CGIAR is a conservation organisation *per se*, but because sustainable increases in productivity are believed to depend on it. However, the processes that supposedly link biodiversity to sustainability are poorly defined. Bioindicators are only now being studied, and this almost exclusively in Europe and North America (Paoletti, 1999). Ecologists have long argued at a theoretical level about whether more complex systems are inherently more stable and this debate now moves into the arena of agricultural systems. One key issue, especially concerning the potential impact of biological control, is the ability of the system to respond to change and still remain functional. This concern has led to the development of the concept of functional groups within the ecosystem, with the underlying idea that any one of several organisms may be able to perform a particular service: pollination or nitrification, for instance (Chapin *et al.*, 1997; Tilman *et al.*, 1997). Thus it is not so much the total diversity of the system that counts but the 'redundancy' built into its vital functional groups. Ideally, a biological control agent should be tested for the risk it poses to members of these functional groups. Yet for most tropical systems, we are scarcely beginning to understand the key processes, let alone to catalogue the members of each group. In the absence of better knowledge, conservation of existing biodiversity is certainly a prudent approach (for Africa: Bennun *et al.*, 1995). However, the issue becomes one of defining an appropriate level of prudence, and looking at the various costs, economic and environmental, of alternative options.

IITA's commitment to the study and preservation of biodiversity is underlined by the fact that IITA Cotonou is the Network Coordinating Institute for the West African region of BioNET. IITA is thus involved in the majority of recent biological control projects in Africa (all executed in collaboration with the relevant national institutions and international institutions). In fact, IITA was also involved in the development of acceptable procedures through the Inter-African Phytosanitary Council (IAPSC) and the Food and Agriculture Organization of the United Nations (FAO). In the course of the biological control projects IITA gained considerable experience in impact assessment, but this experience is mainly restricted to the food webs found in agricultural habitats (or, at most, including adjacent fallows). IITA has never been involved in the testing of indigenous endangered insects and plants.

By reviewing the main biological control projects in which IITA continues to be involved, we shall try to convey some anecdotal evidence of impact (or lack thereof) on indigenous non-target hosts in natural habitats. Non-target species are considered from a broad ecological perspective, which does not focus only on those with popularly recognized 'conservation value'. Concentrating on references to work in Africa, we shall try to show that, when a proper assessment is made of risks and benefits – not just to agriculture, but to biodiversity and the environment as a whole – properly conducted biological control is still an excellent option.

Case studies

Cassava mealybug

The classical biological control project against the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera, Pseudococcidae), established IITA's collaboration with numerous other international organizations (Centro Internacional de Agricultura Tropical (CIAT), CAB *International* (CABI), FAO, Gesellschaft für Technische Zusammenarbeit (GTZ), IAPSC), with universities in Africa, Europe and America, with national research organizations from all over Africa and from other continents (Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)), and with interested donors. The project has had a measurable impact on food production in Africa and stands out as an example of a successful biological control project, the impact of which has also been documented in economic terms (review in Herren and Neuenschwander, 1991; Neuenschwander, 1996) and publicly recognized by the award of the 1995 World Food Prize to the project's leader.

Under the auspices of the IAPSC, predators and parasitoids from South America passed through quarantine at CAB *International*. They were tested, following the 'best practice' then available, to ensure that they were free of diseases and not harmful to other organisms, which generally implied that they were not hyperparasitoids and that they did not feed on bees and silkworms. The information was sent to the various target countries and beneficials were only delivered to government agencies upon presentation of a formal request and import permit. This type of interaction and collaboration became the model for all subsequent biological control efforts in which IITA participated.

In numerous countries, the impact, particularly of *Apoanagyrus* (*Epidinocarsis*) *lopezi* De Santis (Hymenoptera, Encyrtidae), was studied in the field, so that today this is one of the best-researched biological control projects. The evaluation, which covered much of tropical Africa, followed a holistic approach and tried to incorporate the impact on other organisms, such as competitors of the cassava mealybug and their parasitoids and predators. Where *P. manihoti* was abundant, its infestations would spill over on to various nearby plants, on which it was sometimes capable of producing some offspring. As soon as *P. manihoti* had been brought under biological control by *A. lopezi*, however, this mealybug proved to be restricted to the exotic genus *Manihot*. All later studies were therefore carried out on cassava (*Manihot esculenta*), Ceara rubber (*Manihot glaziovii*) and their hybrid, whose leaves are used as a green vegetable.

A food web was documented comprising some 135 species, most of which had never been studied in any detail in Africa. Field and laboratory studies demonstrated the specificity of host acceptance by the female wasp. Only a few parasitoids of a related indigenous mealybug, *Phenacoccus madeirensis* Green, were reared from mummies of *P. manihoti*, indicating that most of these parasitoids could not transfer to the new host, despite its abundance. At the very beginning of these studies, *Anagyrus nyombae* Boussienguet (then under the name *bugandensis*) was found in samples from *P. manihoti*, but later disappeared. The same parasitoid later turned up in yellow pan traps in the forest, but its host to date is unknown (P. Neuenschwander and J. Noyes, unpublished). Similarly, *A. lopezi* was not found on other mealybugs, even those coexisting on cassava.

Another South American parasitoid, *Apoanagyrus diversicornis* Howarth, was released in many countries, but so far has not become established permanently in Africa, either on *P. manihoti* or on any other mealybug. Several oligophagous exotic *Hyperaspis* spp., particularly *Hyperaspis notata* Mulsant, as well as *Diomus hennesseyi* Fürsch (Coleoptera, Coccinellidae), were released in many countries, but were established only locally. Their population levels remained low and they were never found on mealybugs other than *P. manihoti*. Numerous indigenous coccinellids, mainly *Hyperaspis* and *Exochomus* spp., as well as the predatory lycaenid, *Spalgis lemolea* Druce, became abundant when *P. manihoti* first appeared. Predator populations subsided with the collapse of their food source, following successful biological control, and the predators are now found only occasionally in cassava fields. Such non-target effects, driven by food availability, are to be expected in biological control of an exotic outbreak pest.

During the first season after the establishment of *A. lopezi*, when this primary parasitoid was relatively abundant because of the abundance of its host, it was heavily attacked by indigenous hyperparasitoids of local *Anagyrus* spp. A total of 16 species of hyperparasitoids was recorded, with some geographical variation in species composition. As biological control of *P. manihoti* became effective, hyperparasitism rates declined from around 40% to low numbers, indicating a predictable non-target effect on hyperparasitoids (e.g. Neuenschwander and Hammond, 1988).

In summary, this project mainly concerned the introduction of an exotic monophagous parasitoid against an exotic mealybug on an exotic plant genus with no close relatives in Africa, to which the mealybug was restricted when at low population levels. The effect on non-target organisms was most probably neutral, involving a transient effect on indigenous competing predators and hyperparasitoids. Though, in principle, the temporary upsurge of hyperparasitoids might have adversely affected indigenous parasitoids, it seems most likely that density dependence assured timely self-regulation of this impact and eventual relaxation.

Mango mealybug

The accidental introduction of the South Asian mealybug *Rastrococcus invadens* Williams (Homoptera, Pseudococcidae) into West Africa led to a successful biological control project involving the same institutions that were already collaborating in the cassava mealybug project (review in Neuenschwander, 1996). Again, in the early stages of the outbreak, this species attacked a range of host plants but the number of species affected fell sharply as the release of two parasitoids of Indian origin progressed across the infested zone. Within a few years after release, *Gyranusoidea tebygi* Noyes (Hymenoptera, Encyrtidae) covered the entire region and brought the mealybug under effective control in most situations. The second encyrtid parasitoid, *Anagyrus mangicola* Noyes, was more difficult to establish, but is now effective in most towns, where *G. tebygi* was not successful in bringing the host population under total control (A. Bokonon-Ganta and P. Neuenschwander, unpublished results). Again, the same indigenous hyperparasitoids that had reacted to the upsurge of *A. lopezi* transferred to these new encyrtids on mango mealybug. Neither of the Indian parasitoids were ever recovered from other hosts in Africa. In South-East Asia, *A. mangicola* seems to be specific to *R. invadens* (Noyes, 1990) and *G. tebygi* to *Rastrococcus* spp. (Noyes, 1988). Moreover, *R. invadens* seems to be the only member of this genus in West and Central Africa (Williams, 1989).

In conclusion, this biological control project proved to be similar to the one on cassava mealybug, with the exception that *R. invadens* at high densities was more polyphagous than *P. manihoti* and was mainly a pest in towns. Both exotic parasitoids were newly described during the early phases of the project and are only little known from their original home.

Spiralling whitefly

The recent invasion of the spiralling whitefly *Aleurodicus dispersus* Russell (Homoptera, Aleyrodidae) into Africa, following its rapid spread from the Caribbean across the Pacific (Waterhouse and Norris, 1989), set the stage for yet another biological control project with the same institutions. The accidental introduction of *Encarsia ?haitiensis* Dozier and *Encarsia guadeloupae* Viggiani (Hymenoptera, Aphelinidae) made the planned introduction unnecessary (D'Almeida *et al.*, 1998). Nevertheless, the population development of this whitefly was examined on its many hosts. Contrary to the situation with the other two Homoptera, the wide host range has not been much reduced, even after whitefly populations collapsed.

Aleurodicus is part of a small tribe of whiteflies with several African species. These are so rare that we cannot say whether they are attacked by the two introduced parasitoids. The collapse of the exotic population has, however, visibly opened up the system so that more species are again found on different host plants than was the case during the initial infestation, when *A. dispersus* crowded out all competitors (G. Goergen, personal communication). Before the two parasitoids became effective, it was felt that the introduction of an exotic coccinellid would increase the effectiveness of biological control. In particular, *Nephaspis oculata* Blatchley (*amnicola* Wingo) (Coleoptera, Coccinellidae) had been credited with contributing significantly to biological control on several Pacific islands (Waterhouse and Norris, 1989). In view of the newly issued FAO Code of Conduct (FAO, 1996), it was felt necessary to test its host spectrum in greater detail.

The study was carried out in Trinidad (Lopez *et al.*, 1997). It became clear that the biological control agent used in Hawaii as '*N. oculata*' in fact comprised two other species, a new, undescribed one and *Nephaspis bicolor* Gordon. It was therefore decided that *N. bicolor* should be tested. Based on published records, and field and laboratory data, it was concluded that *N. bicolor* and other *Nephaspis* spp. are specialist predators of Aleyrodidae. In Africa, the family Aleyrodidae is represented by 190 described species, some of which are recorded as pests, but the status of most is unknown. It was judged likely that, when introduced, *Nephaspis* spp. would utilize some of the African Aleyrodidae for food. The likelihood that this would lead to extinction of indigenous species was, however, considered insignificant. Eventually, biological control by both *Encarsia* spp. became satisfactory (D'Almeida *et al.*, 1998), so that introducing *Nephaspis* spp. was judged to be too expensive and the species was never brought into Africa.

The fortuitous introduction and eventual efficacy of the *Encarsia* spp. saved biological control practitioners from a potentially insoluble dilemma. Despite the best, and somewhat expensive, efforts by leading institutions, neither the systematics of the biological control candidates nor that of the African aleyrodids were further elucidated. We may wonder what scale of screening would have been needed to reassure all sceptics regarding the safety of these particular biological control agents.

Cassava green mite

The cassava green mite *Mononychellus tanajoa* Bondar (Acari, Tetranychidae) was accidentally introduced into Africa around the same time as the cassava mealybug, and a corresponding biological control project was initiated (review in Herren and Neuenschwander, 1991). A vast range of phytoseiid mites was tested in Colombia with a view to narrowing down the number of species that should be introduced into Africa. Several were introduced, but failed to establish. Later, some of the same species were again imported, but this time from a climatically matching area in north-eastern Brazil. Two of these species, *Typhlodromalus manihoti* Moraes and *Neoseiulus idaeus* (Denmark and Muma) (Acari, Phytoseiidae), were finally established, but their spread proved to be slow. On the basis of laboratory experiments it was concluded that the key to the survival of these phytoseiids was their capacity to survive on alternative food sources, either pollen or non-target tetranychid prey on plants other than cassava. Such feeding would allow them to survive the harvesting of a particular cassava field until they could disperse to a new one planted in the vicinity (Yaninek *et al.*, 1998).

Ten years after the first introductions of phytoseiids from South America, *Typhlodromalus aripo* DeLeon was introduced and proved to be fully successful (IITA, 1996; S. Yaninek, personal communication). *M. tanajoa* prefers the upper parts of the plant, so the tendency of *T. aripo* to shelter in the growing tip may contribute to its specificity. The relatively moderate food consumption of this predator was originally thought to be a negative character but may, in practice, allow it to remain in contact with the host population instead of locally exterminating it. Moreover, the use of alternative plant-based food sources like pollen and exudates from extra-floral nectaries, as well as direct feeding on cassava plant tissue, appear to play a substantial role in the predator's survival and persistence. Unlike the two other introduced phytoseiids, the *T. aripo* strain introduced into Africa has been found only on cultivated cassava. Apart from sustainably reducing an important cassava pest, the project also led to the collection of about 156,000 specimens of 120 species of African phytoseiid mites, among them 30 not yet described (G. de Moraes, personal communication). It is only now, based on this work, that we can even consider quantifying interactions between different mite species.

One might wonder whether this project would have been allowed to proceed today, given that the first two phytoseiids that were established needed non-target hosts on other plants for survival and spread. Moreover, many competing indigenous phytoseiids were not known at the time.

Meanwhile, the ultimately successful predator among about 50 candidate species, *T. aripo*, was seemingly inefficient, if judged on traditional life-table criteria, and proved also to be partly phytophagous. Alternatively, one might speculate that the stricter regulatory environment of today would have focused the search more efficiently on this most specific of candidates, favouring it over the others that may have received priority at least partly because they are easier to rear on some of the mass-produced spider mite species.

Lepidopterous stemborers

This is the most complicated of IITA's biological control projects. It concerns several lepidopterous stem- and earborers (*Sesamia calamistis* Hampson, *Sesamia botanephaga* Tams and Bowden, *Busseola fusca* (Fuller) (Lepidoptera, Noctuidae), *Eldana saccharina* (Walker) and *Mussidia nigrivenella* Ragonot (Lepidoptera, Pyralidae)), which have moved on to maize, having evolved on native grasses, on cereals such as sorghum and millet or on other unrelated host plants (Schulthess *et al.*, 1997). Another stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera, Pyralidae), has been accidentally introduced and is spreading in Africa, sometimes replacing indigenous species of the same genus (Overholt *et al.*, 1997).

Recent studies demonstrate that, contrary to popular belief, wild grasses function as trap plants. They are highly attractive to ovipositing female moths, but larvae developing on them suffer between 95 and 100% mortality, compared with only 70% on maize (Schulthess *et al.*, 1997). It is postulated that, in the humid forest zone, deforestation will lead to an increase of wild grasses that should reduce pest attacks on maize. Moreover, because of their non-determinate growth, these grasses form a more stable habitat for both borers and natural enemies than maize and thereby increase biodiversity to the benefit of the crop. In contrast, in other ecological situations such as the forest–savannah transition, and highlands, where grasses are natural components of plant communities, an increase of acreage planted to maize and concomitant use of nitrogen fertilizer (Sétamou *et al.*, 1995) is expected to reduce biodiversity and increase pest populations on maize. Furthermore, most natural enemy species are poorly adapted to the large-stemmed maize plant and it has become clear that maize stemborers need to be combated in the natural system (Schulthess *et al.*, 1997). In commercial farming systems, where alternative wild host plants are scarce, the prospects for establishment of natural enemies are therefore considered questionable (R. Kfir, personal communication).

The IITA's main thrust in biological control of stemborers is to increase the geographical range of indigenous natural enemy species or strains. Cereal stemborers are attacked by a series of egg parasitoids (*Telenomus isis* Polaszek and *Telenomus busseolae* (Gahan) (Hymenoptera, Scelionidae)) and larval or pupal parasitoids (*Cotesia sesamiae* (Cameron) (Hymenoptera, Braconidae) and *Sturmiopsis parasitica* Currant (Diptera, Tachinidae)) whose importance varies between regions in Africa. Thus, a strain of *C. sesamiae* from Kenya has been introduced, released and established in Benin, while *T. isis* from West Africa has been offered for release in East Africa, where it is absent. Likewise, *S. parasitica* has been introduced from West Africa into South Africa, where it did not occur, and released against *E. saccharina* on sugar cane in 1998 (D. Conlong, personal communication). *Cotesia flavipes* Cameron has been released as a classical, as well as a 'new association', biological control agent worldwide, but did not establish in West Africa (Schulthess *et al.*, 1997). It has low host specificity and also attacks unsuitable hosts (Hailemichael *et al.*, 1997).

The scope for creating new associations, an approach that was thought to have much promise for the future of biological control, is limited by our inadequate knowledge of the taxonomy, biology and distribution of these insects. Thus, several stemborer genera, particularly *Sesamia* and *Busseola*, are in dire need of systematic revision (Maes, 1997). Some parasitoid species have been described only recently or still need systematic treatment, while others, like *C. sesamiae* and *Cotesia chilonis* (Matsumura), are semi-species with partial incompatibility of the crosses (Kimani and Overholt, 1995), adding to the complexity of the system.

It is perhaps not surprising that the impact of biological control agents on non-pest lepidopteran stemborers has rarely been evaluated (Hailemichael *et al.*, 1997). However, even stemborers that are abundant pests on cereal crops are rare in native grasses. It seems likely that indigenous non-pest species in these grasses also occur at low densities (per tiller) and are therefore likely to be protected from overexploitation by introduced parasitoids through density-dependent mechanisms.

Cowpea thrips

A promising new biological control agent against the bean flower thrips *Megalurothrips sjostedti* (Trybom) (Thysanoptera, Thripidae), a devastating pest of cowpea, was discovered by IITA in Cameroon in February 1998 and subsequently identified as *Ceranisus femoratus* Gahan (Hymenoptera, Eulophidae). Eighteen months after this first encounter, *C. femoratus* was found established and spreading up to 150 km from Yaoundé. Apparent parasitism rates both on cultivated and wild growing legumes averaged above 20%, compared with less than 1% parasitism inflicted by *Ceranisus menes* Walker, an indigenous species. This new parasitoid, which had not been found on any thrips species other than *M. sjostedti* in Cameroon, was subsequently brought to IITA Benin for rearing and laboratory testing under standard quarantine regulations (M. Tamò, personal communication). Following testing on *Frankliniella shultzei* Trybom, *Thrips exilicornis*

Hood and *Sericothrips adolfifridrici* (Hood), none of which were attacked, a first experimental release was carried out in mid-July 1999. Preliminary observations indicate successful establishment (M. Tamò, personal communication).

It is interesting to note that *C. femoratus*, a bisexual strain, had formerly been identified as a promising biological control agent (Tamò *et al.*, 1997) and imported from India to quarantine in The Netherlands, where unfortunately the culture died out. The newly discovered strain is parthenogenetic and its recent rapid spread in Cameroon suggests that it may well have been introduced to that country. It must be assumed that the new parasitoid, if efficient, will compete with the local, rather inefficient, egg parasitoid *Megaphragma* sp. (Hymenoptera, Trichogrammatidae), the smallest known insect (Tamò *et al.*, 1993).

Larger grainborer

The case of the larger grainborer, *Prostephanus truncatus* (Horn) (Coleoptera, Bostrichidae), differs in several aspects from the other studies presented here. IITA became involved rather late in the biological control programme, as an observer to the process of importing the key natural enemy and then as an active participant in impact assessment studies. The screening and importation of the natural enemy in question was carried out largely by GTZ, in collaboration with the Plant Protection Service of Togo and the IAPSC.

From an ecological point of view, this case is unusual in that the target insect is known to have a distinctly dual existence: one as a destructive pest of stored maize, cassava and other food products; the other as part of the fauna degrading dead branches in forest habitats. Studies using pheromone-baited flight traps suggest that substantial populations of *P. truncatus* occur in woodland habitats, both in the insect's area of origin – Mexico and Central America – and in outbreak areas in Africa (Borgemeister *et al.*, 1998). Evidently it is in these natural forests that we must be particularly concerned about the potential impact of biological control.

A predator, *Teretrius* (*Teretriosoma*) *nigrescens* (Lewis) (Coleoptera, Histeridae), was identified as the preferred candidate biological control agent for *P. truncatus* at an early stage of comparative studies in Africa and Central America. The initial case for the use of *T. nigrescens* in classical biological control was reviewed at a workshop convened by IITA and FAO (Markham and Herren, 1990). It was built largely on circumstantial evidence of the predator's close association with the target pest – in particular, its co-occurrence in field samples and its response to the aggregation pheromone of *P. truncatus.* It was also built on rather incomplete evidence that storage losses were lower in the pest's area of origin than in outbreak areas in Africa (as reviewed by Markham *et al.*, 1991). Otherwise, prospects for the introduction of this predator were not bright, given that other histerids have not been particularly successful control agents and that even preliminary studies showed that *T. nigrescens* is by no means highly specific as a predator.

The results of further laboratory studies carried out in Europe and cage studies in Togo were then reviewed at a workshop convened by GTZ and FAO (Boeye *et al.*, 1992). Despite evidence that *T. nigrescens* could feed on a variety of soft-bodied insects (including test beneficials such as silk moth immatures and bee brood) when presented in artificial situations and could even feed to some extent on stored produce, the predator was cleared for release, ostensibly on the basis of its 'strong prey specificity' (Boeye *et al.*, 1992).

In the case of the larger grainborer project, there was an explicit effort to examine the possibility of non-target effects. However, it was one of the several ironies of the *P. truncatus*/*T. nigrescens* story that the relevant study was only carried out *after* the predator's introduction to Africa. Protein electrophoresis was used to identify the gut content of predators collected in stores and from pheromone traps set in natural habitats, both in Mexico and in Benin. Fortunately, perhaps, for the further conduct of biological control in Africa, the results from both Africa and the Neotropics showed that, of the rather small proportion of individuals that had traces of protein in the gut, the majority (62.5%) had consumed *P. truncatus* and most of the remainder had reportedly consumed other known cosmopolitan storage pests such as *Sitophilus zeamais* Motschulsky (Coleoptera, Curculionidae), *Tribolium castaneum* (Herbst) (Coleoptera, Tenebrionidae) and *Cathartus quadricollis* (Guérin) (Coleoptera, Cucujidae). There were very few instances of prey which could not be identified, and thus no evidence of significant feeding on non-target species (Camara, 1996). The predator has subsequently been credited with achieving a spectacular reduction in larger grainborer populations in natural woodland in Kenya (Nang'ayo, 1996), and with substantially reducing both pest populations and damage in maize stores in the humid coastal zone of Benin (Borgemeister *et al.*, 1997).

Studies of the kind mentioned here (using protein electrophoresis or DNA techniques) should probably be carried out more often, to assess directly the prey range of predators in their area of origin, before they enter a formal screening procedure. However, there are obvious difficulties with the approach, especially in defining the universe within which potential prey might need to be identified. There is clear evidence that the predator reduced populations of an invading species, *P. truncatus*, in natural habitats where the latter may already have been impacting native species through competition, and it is hard to imagine that such impact could have been alleviated in any other way. However, with increasing concern for unpredictable side-effects of biological control agents on native species, it seems unlikely that candidates with a prey range as potentially broad as that of *T. nigrescens* will be used in future.

Water hyacinth

The water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), the most noxious of all water weeds, has been the object of biological control projects in many countries, using two weevil species, *Neochetina eichhorniae* (Warner) and *Neochetina bruchi* Hustache (Coleoptera, Curculionidae). Other agents were released later; some did not establish and some played a minor role (Julien *et al.*, 1999). In Africa, after the successful campaign in the Sudan, renewed interest in biological control of water hyacinth has led to release of the two weevils (and several other agents) in the Republic of South Africa and from there into the southern tier of Africa, and from IITA Benin into West Africa, the Lake Victoria basin and three rivers in Tanzania (review in Julien *et al.*, 1999).

Previous host range testing for these weevils was very extensive, so that releases into new countries can now be carried out without further testing (Julien *et al.*, 1999). The only other host in the field was the introduced *Pontederia cordata* L., on which complete reproduction proved impossible. The indigenous African Pontederiaceae – *Eichhornia natans* (P. Beauv.), *Monochoria brevipetiolata* Verdc. and *Heteranthera callifolia* Rchb. (Hutchinson *et al.*, 1968) – seem never to have been tested, but as rooted plants they would not appear to be ideal hosts.

While biological control is slowly taking effect and reducing the extent and thickness of water hyacinth cover, competitive pressure on the indigenous flora is subsiding and fish biodiversity is probably resurging to the previous level, at least in connected waterways. In closed waters, it seems likely that some fish, indigenous aquatic plants and their associated fauna could have been eliminated, because biological control arrived too late.

Fungal pathogens against grasshoppers

In the multi-institutional project LUBILOSA (lutte biologique contre les locustes et sautériaux) executed by CABI, the IITA, the CILSS (Comité Inter-Etats de Lutte contre la Sécheresse dans le Sahel) and the GTZ, the indigenous disease-causing fungus, *Metarhizium anisopliae* var. *acridum* Driver and Milner (Deuteromycotina, Deuteromycetes), was developed into a viable commercial product ('Green Muscle') for inundative release by ultra-low-volume application (Lomer *et al.*, 1997; Langewald *et al.*, 1999). This pathogen occurs at low levels in almost identical form across a wide arid belt of Africa, from Mauritania to southern Africa (R. Milner, personal communication). For experimental application and future commercial use, this product was tested extensively in environmental impact studies and found to be specific to Acrididae, Pyrgomorphidae and other smaller Orthopteran families (Lomer *et al.*, 1997). As such, it is a far more specific and environmentally less disruptive product than any insecticides commonly used for acridid control (Peveling *et al.*, 1999). This was recently confirmed by the FAO Locust Pesticide Referee Group, which included 'Green Muscle' on the list of recommended products for locust control, where it was the only product rated as posing no known environmental risk of any sort and no threat to human health (R. Bateman, personal communication).

The question arose, however, as to whether its widespread use would endanger the indigenous low density, endemic grasshoppers of the Karoo (R. Price, personal communication). The fact that these grasshoppers occur at low densities and are widely dispersed, though in a restricted area, might indicate that they would not suffer to a great extent from more localized sprays of the fungal pathogen. While some will be killed, the proportionately higher kill of their competitors is likely to mitigate this loss. Moreover, 'Green Muscle' has been selected against acridids, while pyrgomorphids, for instance, are less susceptible. Whether the same is true for the endemic South African grasshoppers is not known.

If locust control becomes as efficient as it is hoped, then the disappearance of dense locust populations will itself have a strong effect on other species. Numerous bird species, especially migrants, rely on this abundant food source in their winter quarters (Crick, 1990). It would be hard to argue, however, that a reduction in locust levels by biological control is likely to have a more negative effect on birds (or other non-target species) than conventional spraying. During the last major locust control campaign, from 1986 to 1989, 1.5 million litres of pesticides were applied, at a cost of US$300 million (Symmons, 1992).

Discussion

The case studies presented here document an evolution towards increasing caution by biological control practitioners in Africa. This is being complemented by a continuing effort to update the regulatory framework provided by the IAPSC. We have noted several instances where, if the same project were to be carried out in today's context, things might have been done rather differently. However, in only one instance would this greater caution have substantially affected the outcome of the project: against the larger grain borer, the histerid predator probably would not have been introduced at all. The key question is now how far we should follow North America, Europe and Australia down the road of more comprehensive pre-introduction testing of candidate natural enemies, and what the implications would be for preservation of biodiversity.

Weed biological control specialists have been relatively successful in defining procedures to look at the risks both to crops and to indigenous flora, starting with the most closely related taxa and 'working outwards'. However, we know so little about the taxonomy of non-target relatives of most crop pests in Africa that it would be an immense task just to define where to start with such procedures for arthropods. Moreover, as Sands (1997) points out, it is far less obvious what constitutes an appropriate 'safety test' for arthropod natural enemies and, effectively, each test must be 'tailor-made' to take account of the behavioural characteristics of each candidate, especially *vis-à-vis* its reaction to host/prey cues, host plant cues and other environmental stimuli and conditions.

In general, we accept the proposition that the previous model of unbranched food chains being the norm was oversimplified (Strong, 1997), and that we need to look more carefully at the possible branches and web connections, which are often more diverse in natural than in agricultural environments (Valladares and Salvo, 1999). If this leads to more careful preparatory work, to elucidate biology and ecology, being done in the country of exploration, we wholeheartedly support this development. Such work can also be used as a vehicle for strengthening 'South–South' collaboration, as was the case for studies in Brazil associated with the biological control effort against cassava mites in Africa. However, if this road leads in the direction of ever more costly, prescriptive formal screening, in the course of third-party 'quarantine', we would be much less enthusiastic. Biological control is an option that should not be 'priced out of the market' by the imposition of unrealistically stringent controls.

Whether we like it or not, costs are a key issue, and not just the costs to agriculture or the natural environment, but also the social cost. Samways (1997), despite highlighting some instances where biological control has seemingly provided the only viable solution to urgent conservation problems, seeks to define biological control as primarily an 'economic activity'. The implication is that biological control is selected in agriculture on the basis of narrow cost–benefit considerations, and it is further implied that, once a wider, ecologically based risk assessment is carried out, the potential ecological costs will be found to be too high. This assumes, firstly, that the risks posed to biodiversity by biological control are substantial and, secondly, that intensified agricultural technology can provide alternatives. Yet in several of the case studies presented here, there was simply no viable alternative.

As pointed out in the introduction, socio-economic forces determine that a grave threat to a low market value food staple, such as cassava, in Africa is simply met by additional clearing of forest (with devastating impact on biodiversity). Biological control is being adopted for water weeds and proposed for locusts and grasshoppers precisely to get away from the environmental and social hazards of broad-scale spraying of the environment. In Africa, many farmers can neither read the hazard warning labels on pesticides nor afford protective clothing. Moreover, many African countries lack the appropriate regulatory framework and the means to enforce it. In these circumstances, any move towards using more pesticides implies a substantial increase in the health hazard to farmers and consumers. These are substantial social risks that even a die-hard conservationist should weigh in the balance against the supposed environmental risks of biological control.

In conclusion, in Africa we are still a long way from the 'gardenification' of conservation proposed by Janzen (1998) in which biodiversity is preserved in carefully managed packages, and, by implication, the risks of interventions such as biological control are easier to define. In the meantime, we must maintain a cautious approach that uses all ecologically sound reasoning available to make good decisions on the selection of biological control agents. However, the regulatory framework should not be made so prescriptive and cumbersome that biological control ceases to become an affordable option and is replaced by alternatives that are patently more destructive to natural environments. Biological control is a powerful instrument, particularly in Africa, where its implementation is favoured by the tolerance of relatively high economic thresholds and a rich surrounding environment offering shelter and alternative food sources for natural enemies, at no cost to the farmer.

Above all, in assessing risks and benefits, we need to include a social dimension, along with economic costs and benefits, and ecological risk assessment. As Cohen (1997) has forcefully pointed out, we may soon be approaching the limits of the earth's human carrying capacity but, long before that, we are facing hard decisions about poverty and equity, and how these social parameters affect natural resource management decisions. Malnourished people, living in poverty, on a deteriorating resource base, are not well placed to make sound long-term decisions about protecting their natural environment. Imposing on such people just one subset of environmentally sensitive values, developed in the 'North' under quite different circumstances, is likely to have quite the opposite impact on biodiversity from the one intended.

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8

Rhinocyllus conicus: Initial Evaluation and Subsequent Ecological Impacts in North America

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Abstract

Renewed debate over the risk of non-target effects in biological control reflects, in part, the recent quantification of direct and indirect ecological effects of the flowerhead weevil, *Rhinocyllus conicus* Fröl., in North America. To help resolve the issue, we review the published data for *R. conicus* from both Europe and North America: pre-release (1961–1968), post-release (1969–1985) and more recent (1986–1999). Our aim was to determine the extent to which host range expansion on to native North American species, and the associated ecological effects, were predicted or predictable. Our overall conclusion is that more was known than is generally realized, yet more information would have been required to complete the initial assessment of ecological consequences. Three important points emerge. First, the potential effect of *R. conicus* on native North American species was not a major element of the testing programme. Second, the host range expansion observed is consistent with the pre-release and early post-release data, and so was predictable, if not predicted. The pre- and early post-release data showed that *R. conicus* could feed and develop on multiple *Cirsium* species, including two North American species. Third, we found that the studies needed to quantify the likely magnitude of feeding by *R. conicus* on North American *Cirsium* species, and thus the ecological consequences of that feeding, were not done. Instead, inferential arguments were used to suggest that any feeding by *R. conicus* on North American species would not be substantial. We conclude that there were sufficient data, which suggested that North American *Cirsium* species would be acceptable

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host species, to have warranted further testing to define and quantify the potential ecological side-effects of introducing *R. conicus* to North America. Contemporary concerns should now mandate such tests.

Introduction

The risks associated with the practice of biological control, especially the potential for harmful ecological effects on non-targeted native species, are being debated again (see Secord and Kareiva, 1996; Simberloff and Stiling, 1996, 1998; Frank, 1998; Thomas and Willis, 1998). The issue is not new (e.g. Simberloff, 1981, 1992; Howarth, 1983, 1991). In fact, the importance and the need of doing more quantitative evaluations of potential risk to non-target native species was argued by several biological control practitioners over 15 years ago (Andres, 1985; Pemberton, 1985a,b; Turner, 1985). Several countries, such as Australia and New Zealand, have instituted a clear legislative process to identify risks, to involve all affected parties and to ensure that non-target impacts are minimized (New Zealand Government, 1994; Withers *et al.*, 2000).

In this chapter, we will review the evidence available to evaluate the specific case of the introduction of *Rhinocyllus conicus* Fröl. (Fig. 8.1) into North America. This Eurasian weevil was released for the biological control of true thistles, especially those in the genus *Carduus*. Recent evidence that

Fig. 8.1. *Rhinocyllus conicus* on Platte thistle (*Cirsium canescens* Nutt.) at Arapaho Prairie, Arthur County, Nebraska, USA.

R. conicus populations are increasing in nature preserves and National Parks in the central USA (Louda *et al.*, 1997, 1998; Louda, 1998), and that these populations are having a significant impact on native plant and insect species within the preserves (Louda *et al.*, 1997; Louda, 2000a; Louda and Arnett, 2000), has rekindled earlier apprehensions about the environmental safety of classical biological control (Howarth, 1991; Secord and Kareiva, 1996; Simberloff and Stiling, 1996).

Specifically, we will examine the evidence developed on this insect and its host plant interactions in Europe before, and in the 15 years after, its release in North America. Then, we will summarize the more recent findings. Thus, our purpose is to determine the extent to which the host range expansion on to native North American *Cirsium* species, and the ecological effects recently associated with this expansion, were predicted or predictable from the published data used to evaluate economic and environmental risk. Our overall conclusion for this case is that more was known than is generally realized, and yet more information would have been required to effectively assess potential ecological consequences.

The common name 'thistle' is customarily applied to species in the Tribe *Cardueae* of the *Asteraceae* (*Compositae*), and the term 'true thistle' is sometimes used to refer to the spiny species of the Subtribe *Carduinae*. Some ten different 'true thistle' species in four genera of western Palaearctic origin (*Carduus*, *Cirsium*, *Silybum* and *Onopordum*) have been accidentally introduced into North America, Australia and New Zealand (Julien and Griffiths, 1998). No native *Carduus* species occur in North America and most indigenous Nearctic true thistles belong to the genus *Cirsium*. The *Carduus nutans* group is taxonomically difficult, and it includes several species or subspecies (Desrochers *et al.*, 1988). In this chapter, we use *C. nutans* L. to refer to all of the taxa in this complex group.

In North America, the weediness of exotic true thistles was viewed as an agronomic problem (e.g. Dunn, 1976; McCarty, 1978). So, both the US Department of Agriculture (in 1959) and the Canadian Department of Agriculture (in 1961) initiated biological control programmes against exotic thistles, starting with broad surveys of the insects and pathogens on the *Cardueae* in Europe (Zwölfer, 1965; Boldt, 1978; Dunn, 1978). Between 1961 and 1966, 2283 populations or stands of 16 genera in the tribe, including 1354 in the Subtribe *Carduinae*, were surveyed from western France to eastern Austria, and from southern Germany to northern Italy and northern former Yugoslavia (Zwölfer, 1965). Over 120 species of insects were associated with true thistles in the genera *Carduus*, *Cirsium*, *Silybum* and *Onopordum* in the western portion of their indigenous Eurasian range (Zwölfer, 1965; Redfern, 1983). Boldt (1978) reported that some 40 insects were endophytic on *C. nutans* in Italy. On the basis of the surveys and early tests, *R. conicus* was selected as the first agent to be released in North America for the biological control of exotic thistles, especially those in the genus *Carduus*. Weevils, collected in the upper Rhine Valley in eastern France, were first released in Canada in July 1968 on musk (nodding) thistle (*C. nutans*) near Regina, Saskatchewan, and on plumeless thistle (*Carduus acanthoides* L.) near Belleville, Ontario (Harris and Zwölfer, 1971). In 1969, introductions from eastern France began in the United States, with releases in California, Montana, Nebraska and Virginia (Hawkes *et al.*, 1972; Kok, 1974; Kok and Surles, 1975; Rees, 1977, 1978, 1982, 1991; McCarty, 1978; Surles and Kok, 1978; McCarty and Lamp, 1982). In Nebraska, weevils from Mulhouse, France, and possibly some from Rome, Italy, were released in 1969 and between 1972 and 1974 on *C. nutans* near Lincoln and Grand Island (McCarty, 1978; L.A. Andres, unpublished results). The weevil was then actively redistributed in southern and eastern Nebraska (McCarty and Lamp, 1982). Redistribution of *R. conicus* in the United States continues (e.g. Boldt and Jackman, 1993; Buntin *et al.*, 1993).

The history of research on *R. conicus* in Europe and North America can be divided into three periods, including the pre-release period of research in Europe (1961–1968), the early post-release period (1969–1985) and the more recent period of research (1986–1999). After reviewing the natural history of *R. conicus*, we will summarize the findings relevant to evaluation and prediction of post-introduction performance from each of these periods. We will then address the general question of whether the state of knowledge at pre-release and early post-release was sufficient to predict both the occurrence of feeding and the magnitude of ecological impact by *R. conicus* on native thistles and their adapted floral insects. We contend that such retrospective studies can be used to evaluate and improve future efforts in biological control.

Natural history of *Rhinocyllus*

The indigenous geographical distribution of *R. conicus* includes central and southern Europe and North Africa (Hoffmann, 1954), as well as Asia Minor (Schaufuss, 1915). Preferred habitats of thistles in Europe, according to Zwölfer (1964), are in dry and warm localities below elevations of 600 m. Mating and oviposition activity occur in spring and early summer, following adult emergence from overwintering in litter and sheltered sites and a pre-oviposition feeding period of varying length. Eggs are laid externally, either individually or in small clusters, on the lower surface of the involucral bracts of young flowerheads (Rees, 1977, 1982; Zwölfer and Harris, 1984). The life cycle is well documented. Larvae feed on the florets, the developing receptacle, callus tissue produced near the feeding site (Shorthouse and Lalonde, 1984), and sometimes into the peduncle under the head (Zwölfer and Harris, 1984). At the end of the fourth instar, the larva forms an ovoid cell with hard, frass-packed, black walls and pupates (Shorthouse and Lalonde, 1984; Zwölfer and Harris, 1984). Development, from egg to teneral adult, took 45–55 days in the Swiss Jura (Zwölfer and Harris, 1984) and 39–62 days in the Gallatin Valley, Montana, USA (Rees, 1982). Teneral adults usually remain within the pupation cells for several weeks before dispersing to find overwintering sites (Zwölfer and Harris, 1984). The number of generations per year can vary, from one in the Apennine Mountains of Italy (Mellini, 1951) and southern Europe (Aeschlimann, 1999), to a partial second generation in the upper Rhine Valley and eastern Austria in central Europe (Zwölfer, 1967).

In Europe, *R. conicus* overlaps with a large number of floral herbivores (Zwölfer, 1965) that may cause substantial mortality (Zwölfer, 1978, 1979). For example, in flowerheads with either *Urophora solstitialis* L. (Tephritidae) or *Larinus sturnus* Schall. (Curculionidae), *R. conicus* mortality averaged 70–90% (Zwölfer, 1978; Zwölfer and Harris, 1984). In North America, larval survivorship is strongly density-dependent (Surles *et al.*, 1975; Rees, 1977; Dowd and Kok, 1981a; Goeden and Ricker, 1985), suggesting that intraspecific competition can cause larval mortality (> 80%) within heavily infested inflorescences.

The natural enemy complex is extensive in both Europe and North America. In Europe, Zwölfer and Harris (1984) listed six larval and pupal parasites, plus an egg parasitoid (Mellini, 1951). Parasitism levels in Europe were high, especially by *Bracon* sp. (43–71%), *Bracon urinator* L. (40–50%) and *Exeristes roborator* F. (13–43%). Natural enemies reported in North America include: parasitoids (1 adult, 10 larval-pupal), predators (a reduviid, a neuropteran, salticid and thomisid spiders) and parasites (a mite, two bacteria and a fungus) (Goeden and Ricker, 1977, 1978; Dowd and Kok, 1981b). Reported levels of parasitism in the USA are very low (< 3%) (Surles, 1974; Surles *et al.*, 1975; Goeden and Ricker, 1977; Rees, 1977; Puttler *et al.*, 1978; Dowd and Kok, 1981a, 1982, 1983; Smith and Kok, 1983). Finally, some intra-guild predation occurs in Europe. Two lepidopterans that develop on floral tissues and achenes within *C. nutans* flowerheads (Pyralidae: *Homoeosoma nebulellum* Hb., *H. binaevellum* Hb.) reportedly also feed on any insect larvae that they encounter, including those of *R. conicus* (Zwölfer, 1978). In North America, related lepidopteran larvae (*Homoeosoma* spp.) occur within flowerheads of native *Cirsium* species (Lamp and McCarty, 1981; Louda and Potvin, 1995; G. Balogh, personal communication). Rees (1977, 1978) found no evidence of feeding by *Homoeosoma electellum* (Hulst.) on *R. conicus* in Montana, but no direct test has been done.

Pre-release studies in Europe (1961–1968)

Study of *R. conicus* as a potential biological control agent for exotic thistles in North America, particularly *Carduus* species, included both field studies of occurrence and host use and laboratory studies of adult behaviour and larval performance. Zwölfer and Harris (1984) synthesized most of the results for *R. conicus* available before 1984.

Early field studies

Field collection records of *R. conicus* in Europe (Table 8.1) show that eggs or larvae of *R. conicus* were found on five out of nine *Carduus* species (55.6%) and two out of 16 *Cirsium* species (12.5%), as well as on *Silybum marianum* (L.) Gaertner and *Onopordum acanthium* L. (Zwölfer, 1967). Adults were also found on *Carduus sanctae-balmae* Lois, at Toulon in southern France, and on *Cirsium vulgare* Ten., at Nantes in western France and at Châteauroux in central France, but not on *C. vulgare* in eastern France or in the Rhine Valley. *R. conicus* larvae and adults were found on *C. nutans* everywhere except in southern France and north-eastern Spain. Other host plants in the literature included *Galactites tomentosa* Moench and four more *Cirsium* species: *Cirsium eriophorum* (L.) Scop., *Cirsium canum* (L.) All., *Cirsium anglicum* Lob. and *Cirsium chrysacanthum* Ball. These literature records, however, could not be confirmed in the early surveys (Zwölfer, 1965; Zwölfer and Harris, 1984).

The field records for Europe suggested a clear preference of *R. conicus* for *Carduus* species over other accepted plant species. Zwölfer (1967) pointed this out:

> The genus *Carduus* is by far preferred over the host genera *Cirsium*, *Silybum*, or *Onopordum*. The genus *Cirsium* has been investigated much more intensively than the genus *Carduus*, but nevertheless 75% of the records of adults and 80% of the records of larvae of *R. conicus* originate from *Carduus* species.

R. conicus was observed on three out of 16 *Cirsium* species investigated. The percentage of samples containing eggs or larvae of *R. conicus* varied from 20 to 60% within the genus *Carduus*, below 5% in the genus *Cirsium*, and below 10% in the genera *Silybum* and *Onopordum*. Unlike for *Larinus* spp., no evidence of intraspecific differentiation was observed. So, Zwölfer (1967) suggested that regional differences in host plant association of *R. conicus* could be related to host preference and phenology.

Population phenology of *R. conicus*, initiated by adult emergence from overwintering sites, varies with latitude and elevation within Europe and the Mediterranean. For example, in the upper Rhine Valley in the north, Zwölfer (1964, 1967) found that *R. conicus* adults were active from the first half of May, when they were abundant, until August. Larvae were found in flowerheads from late May until August, and pupae occurred from mid-July to September (Zwölfer, 1964, 1967; Zwölfer and Harris, 1984). A partial second generation sometimes occurred for individuals that completed development early, when day length was greater than 16 h (Zwölfer, 1967; Zwölfer and Harris, 1984). Additionally, in the Apennine Mountains north of Florence, Mellini (1951) observed a relatively late onset of all stages: oviposition in early July, larval development in July/August and pupation in late August. In the Mediterranean climate region, for example near Toulon and Orange in southern France and Gerona in northern Spain, Zwölfer (1967) found over-wintered *R. conicus* adults emerging very early, from mid-April, and eggs were found from early May. In summary, *R. conicus* in the Mediterranean climatic area were active several weeks ahead of those in the more continental areas or higher elevations, and they were reported to have a shorter activity period.

Early laboratory studies of host acceptance, preference and performance

The plant species tested in the screening trials included primarily cultivated plants, agricultural crops and horticultural species, plus European thistles (Zwölfer, 1964, 1967, 1969; Zwölfer and Harris, 1984). All the tests were made with field-collected adults originating from *C. nutans* from eastern France. In no-choice feeding tests, where adult weevils were offered leaves of a potential host plant, no feeding occurred on the cultivated non-*Astereae*, but 12 of the 16 European species of *Carduinae* offered were fed upon. One North American *Cirsium* (*Cirsium undulatum* Spreng.) was screened in one small adult feeding trial in Canada (*n* = five weevils). The leaves of this species were accepted, but only at the ‘slight and inconsistent feeding’ level (Zwölfer, 1967), the same level as European *Carduus tenuiflorus* Curtis, *S. marianum* and *O. acanthium* (Zwölfer and Harris, 1984). Interestingly, the five weevils in this trial on *C. undulatum* died more rapidly than did those on the leaves of other thistles tested (Zwölfer, 1967; Zwölfer and Harris, 1984).

Some feeding was noted in preference (i.e. ‘choice’) tests, where adult weevils were offered leaves of both *C. nutans* and another plant in the Tribe *Cardueae*, i.e. *Carlina vulgaris* L., *Carthamus tinctorius* L. and *Cnicus benedictus* L., as well as 12 of 14 species in the Subtribe *Carduinae* (Zwölfer, 1964). Among the *Carduinae*, two results are striking. First, the preference for two (16.7%) of the 12 species (*Carduus crispus* L., *Cirsium acaule* (L.) Scop.) was actually greater than that for *C. nutans*. Second, the thistles fell into two groups. The highly preferred group included (in rank order): *C. crispus*, *C. acaule*, *C. nutans* and *Cirsium vulgare*. The less preferred group included (in rank order): *Cirsium arvense* (L.) Scop., *Cirsium rivulare* (Jacq.) All., *Cirsium palustre* (L.) Scop., *Carduus personata* (L.) Jacq., *S. marianum*, *Cirsium oleraceum* (L.) Scop., *Carduus tenuiflorus* and *O. acanthium* (Zwölfer, 1964). These two groups are clearly not defined by host plant genus.

In oviposition and larval development tests, the data included records of eggs laid in laboratory feeding trials on leaves, and a no-choice field test of oviposition and development. The latter test was done in the garden at Delémont, Switzerland, on four of the eight European thistles with

Table 8.1. Field records of *Rhinocyllus conicus* (modified from Zwölfer, 1965, 1967; Zwölfer and Harris, 1984).

	1961–1966			1961–1982		
	Populations sampled	% samples with larvae[a]	% samples with adults[a]	Populations sampled	% samples with larvae[a]	% samples with adults[a]
Echinopinae						
Echinops (4 spp.)	25	0	0	41	0	0
Carlinae						
Carlina (3 spp.)	85	0	0	158	0	0
Xeranthemum (1 sp.)	5	0	0	7	0	0
Centaureinae						
Serratula (1 sp.)	16	0	0	17	0	0
Centaurea (17 spp.)	750	0	0	950	0	0
Microlonchus (1 sp.)	8	0	0	11	0	0
Crupina (2 spp.)	5	0	0	6	0	0
Leuzea (1 sp.)	5	0	0	9	0	0
Carthamus (1 sp.)	30	0	0	47	0	0

Carduinae						
Arctium (4 spp.)	60	0	0	106	0	0
Jurinea (1 sp.)	—	—	—	2	0	0
Staehelina (1 sp.)	5	0	0	8	0	0
Galactites (1 sp.)	10	0	0	12	0	0
Carduus nutans	109	57.5	60.0	157	49.0	50.3
C. nigrescens	3	33.3	100.0	3	33.3	100.0
C. personata	25	33.0	38.0	28	35.7	42.9
C. crispus	20	40.0	20.0	30	26.7	13.3
C. sanctae-balmae	6	0	50.0	6	0	50.0
C. pycnocephalus	12	20.0	30.0	17	23.5	35.3
C. acanthoides	39	0	0	55	0	3.6
Two other *Carduus*	40	0	0	44	0	0
Cirsium vulgare	142	0	0.8	225	6.2	7.1
C. palustre	47	4.0	0	60	3.3	0
C. setosum	—	—	—	3	33.3	0
C. arvense	475	3.5	4.0	550	2.9	3.8
13 other *Cirsium*	300	0	0	356	0	0
Silybum marianum	14	8.0	0	23	17.4	26.1
Cynara scolymus	—	—	—	4	0	0
Onopordum acanthium	42	5.0	10.0	47	4.2	8.5
Two other *Onopordum*	5	0	0	19	0	0

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[a] Percentage of local populations sampled for the presence of larvae or adults of *R. conicus*.

R. conicus oviposition recorded from the field: *Carduus nutans*, *C. personata*, *Cirsium arvense* and *C. palustre*. Each of these species supported complete development. Zwölfer (1967) noted that 'The adults emerging from *C. arvense* and *C. palustre* were, however, about 10% smaller than their parents which originated from *C. nutans*'. Thus, this early screening trial showed that the two European *Cirsium* species were adequate hosts, even though they were much less preferred than *C. nutans* in adult feeding trials (Zwölfer, 1964). No oviposition tests or larval development tests were carried out on any North American *Cirsium* species. Also, no multiple-choice oviposition preference and larval development tests were done to determine the relative ranking of potentially acceptable European or North American thistle species.

In summary, the early trials substantiated that feeding by *R. conicus* was restricted to the Subtribe *Carduinae*, and they suggested that some species of acceptable thistle host plants were preferred over others. Since none of the agricultural crops and horticultural species tested was used by the weevil, the decision was taken by the Canada Department of Agriculture and the US Department of Agriculture, Agricultural Research Service, to release the weevil on exotic thistles in Canada (*C. nutans*, *C. acanthoides*) and in the United States (*C. nutans*, *S. marianum*). Redistribution of *R. conicus* continued, even though some feeding on non-target *Cirsium* species was recorded very early and there was 'considerable opposition to the introduction to North America of biocontrol agents for thistles on the grounds that they may also damage native *Cirsium* spp.' (Zwölfer and Harris, 1984).

Early post-release studies (1969–1985)

After release, studies of the host associations of *R. conicus* in Europe were continued, and studies of the biology and feeding of *R. conicus* on its targeted host plants were done in North America.

Field studies in Europe

Additional surveys were carried out during 1981 (see Table 8.1). The patterns were consistent with the previous studies, although *R. conicus* adults were also documented on *Carduus acanthoides*. In addition, the rate of attack recorded on *Cirsium vulgare* was higher than previously, most likely because sampling increased in south-western France. Occurrence of *R. conicus* on *C. vulgare* was higher in south-western France than in north-eastern France, Austria and Germany (Zwölfer and Preiss, 1983). In total, 4 out of 17 *Cirsium* species (23.5%), and seven out of nine *Carduus* species (77.8%), were recorded as hosts of *R. conicus* during 1981. The phenology of *R. conicus* in North America was quantified and also found to vary with latitude, with earlier emergence and activity in the south. In the Gallatin Valley of Montana, USA, overwintered adults were observed aggregating and mating on musk thistle (*C. nutans*) from mid to late May, and newly emerged adults were found primarily in late July and early August (Rees, 1982). Alternatively, further north, newly emerged adults were observed in late July to early August in southern Ontario, but not until August in Saskatchewan (Harris, 1984).

A major change occurred during this period in the general interpretation of the variation in host plant association of *R. conicus* in the field. Before *R. conicus* was released in Canada in 1968, host preference and possibly host phenology were thought to determine host association (Zwölfer, 1967). However, by 1984, ecotypic differentiation among host-related strains ('biotypes') of *R. conicus* was widely, if not universally, accepted as the main determinant of host association (Zwölfer and Harris, 1984). This shift was initiated by Goeden's (1978) observation that the response of *R. conicus* to its host plants in southern California varied. Weevils from *Carduus pycnocephalus* L. consistently preferred to oviposit on *C. pycnocephalus*, whereas those from *S. marianum* preferred *S. marianum.* Goeden (1978) hypothesized that two 'host races' of *R. conicus* existed in California. He then hypothesized that the earlier attempt to establish *R. conicus* on milk thistle (*S. marianum*) in northern California (Hawkes *et al.*, 1972) had failed because the weevil biotype and weed species were mismatched (Goeden, 1978; Goeden *et al.*, 1985).

In Europe, Goeden's hypothesis stimulated a re-assessment of host records for *R. conicus.* Zwölfer and Preiss (1983), for example, also concluded that *R. conicus* was divided into five 'host race' biotypes: (i) *S. marianum* biotype; (ii) *Carduus nutans* biotype, also occasionally found on *Cirsium* spp., which was the most widespread and presumably most ancient biotype, (3) *Carduus pycnocephalus* – *C. tenuiflorus* biotype; (iv) *Cirsium arvense* biotype, which was rare in Europe; and (v) *Cirsium vulgare* biotype in western France, which was also occasionally found on *Carduus nutans.* Thus, Zwölfer and Preiss (1983) rejected the weevil – host plant synchrony hypothesis (Zwölfer, 1967) to explain variation in host plant use among regions, and they accepted the innate preference hypothesis instead. They suggested that preference was driven by selection for resource predictability, consistent with the resource concentration hypothesis (Root, 1973), and this determined host plant association and its geographical variation.

At this point, definitive evidence for five clearly differentiated, genetic host races (biotypes) was not available, and some conflicting evidence existed. For example, *R. conicus* from *Cirsium vulgare,* evaluated in a multiple-choice oviposition test, unexpectedly laid as many eggs on *Carduus nutans* as they did on *Cirsium vulgare* (Zwölfer and Preiss, 1983). Also, Jessep (1981) reported that, in New Zealand, *R. conicus* from Canadian *Carduus nutans* successfully colonized *Carduus pycnocephalus*, *C. acanthoides* and *C. tenuiflorus*, as well as *C. nutans.* Moreover, the role of interspecific variation in the availability of flowerheads was not evaluated, even though it was known that intraspecific variation in flowerhead size influenced oviposition in both *S. marianum* and *C. vulgare* (Zwölfer and Preiss, 1983).

It seems clear that the wide acceptance of host-plant biotypes, and perhaps of resource concentration, as predictive of host use, had a major influence on the interpretation of the data. These perspectives lead to the expectation of insignificant levels of non-target feeding on native North American *Cirsium* species by *R. conicus* from *C. nutans.* The existence of host-plant biotypes in *R. conicus* has been challenged recently (Klein, 1991; Klein and Seitz, 1994).

Laboratory and greenhouse studies of preference and performance in North America

Kok and his colleagues in Virginia experimentally substantiated the oviposition preference of *R. conicus* from *C. nutans* in Europe for *C. nutans* over *C. acanthoides* in its new environment (Surles and Kok, 1977), as expected. They found that oviposition was better synchronized with *C. nutans* than with *C. acanthoides* in Virginia. Also, larval crowding decreased survival more in the smaller flowerheads of *C. acanthoides* than in the larger ones of *C. nutans* (Dowd and Kok, 1981a). Second, Smith and Kok (1985) found that temperature influenced larval development and mortality. The threshold temperature for hatching was 11°C, and the threshold temperatures for development were between 16 and 20°C, depending on the stage. Third, Dowd and Kok (1983) documented the influence of plant quality on weevil success. In the greenhouse, weevils developing in flowerheads of musk thistle (*C. nutans*) plants that were fertilized or well-watered, compared with unfertilized or dry, tended to survive better and they developed into significantly larger adults. Also, phytosterols (especially sitosterol), which are found in highest concentrations in the flowerhead buds, were necessary for complete larval development on artificial diets (Rowe *et al.*, 1985). These studies suggested that preference and synchronization, based on physical conditions and host plant quality, could influence host plant use by *R. conicus* in the field in North America.

Garden plot and field studies in North America

In Canada, field studies showed that oviposition was concentrated at the beginning of the flowering season. Although egg distribution was aggregated, the larval distribution was even more aggregated, and the degree of aggregation varied significantly among years (Zwölfer and Harris, 1984). Variance-to-mean ratios ranged from 1.84 to 7.99 in pasture and from 1.0 to 11.37 in gravel spoil plots over the first 10 years. Also, the maximum number of *R. conicus* maturing in a *C. nutans* head was correlated with its size. Growing conditions again appeared important. For example, the degree of aggregation was inversely correlated with spring soil moisture. Day length affected the development of a second partial generation. Newly developed adults that had emerged early, by mid-June (> 16 h light), were observed mating. Finally, a low incidence of parasitism by a wide variety of larval and pupal parasitoids was reported in Canada (Zwölfer and Harris, 1984).

In Virginia, establishment by the *R. conicus* imported from *C. nutans* in eastern France was more successful on *C. nutans* than on *C. acanthoides* (Kok, 1974; Surles *et al.*, 1974; Kok and Surles, 1975), possibly due to synchrony. Total mortality for all immature stages of *R. conicus* on *C. nutans*, at 11 release sites in Virginia, averaged 68%, ranging from 56.6% to 95.3% (Surles *et al.*, 1975). Egg and early instar larval mortality (58.3%) was caused primarily by wind and rain. Late larval and pupal mortality (9.7%) was caused by parasitism (3.6%), larval crowding and unknown factors (Surles *et al.*, 1975). In both 1973 and 1974, weevils reduced the number of viable seeds in the terminal and first lateral heads and total seed production by 35–36% per *C. nutans* plant. However, they only reduced viable seed by 0.2% per *C. acanthoides* plant, due to low infestation rates (Surles *et al.*, 1974; Surles and Kok, 1978). A phenological model of the interaction of *R. conicus* with *C. nutans* in Virginia (Smith *et al.*, 1984) demonstrated that temperature could have a major influence on the synchrony of the host plant and weevil, and so on the magnitude of their interaction.

In California, Goeden (1978) and Goeden and Ricker (1977, 1978) found evidence consistent with the host race hypothesis. *R. conicus*, collected from *S. marianum* in southern Italy, established successfully on *S. marianum* in southern California (1971–1974), even though earlier releases of weevils from *C. nutans* in eastern France had failed to establish on *S. marianum* in northern California (Hawkes *et al.*, 1972; Goeden, 1978). In 1978, another establishment of the southern Italian form of *R. conicus* was made on *S. marianum* in Fall County, Texas, USA, using weevils from *S. marianum* in California (Boldt and DeLoach, 1985). Clearly, these observations suggest that genetic variation occurs among populations of *R. conicus*. Interpretation of how that variation is partitioned is now being revised (Klein, 1991; Klein and Seitz, 1994).

In the Gallatin Valley in Montana, USA, Rees (1977, 1978) reported that after 5 years *R. conicus* had spread throughout 1280 km^2 in the valley, suggesting a rate of spread of up to 19 km year^{-1}. Damage to the primary, terminal flowerheads of *C. nutans* subsp. *macrocephalus* reduced their seed production, but the later secondary heads were missed (Hodgson and Rees, 1976; Rees, 1978). Interestingly, the length of the oviposition period, when mating weevils were observed, varied between years: 10 days in 1975, 39 days in 1976 (21 May–28 June) and 27 days in 1977 (Rees, 1978). Also, mortality from intraspecific larval competition increased from 23.3% to 82.5% as the number of *R. conicus* larvae increased from 15.6 to 21.3 per head (Rees, 1977). The sunflower moth, *Homoeosoma electellum* (Hulst.), was observed to feed within the heads but, unlike the European situation, no evidence of attack on *R. conicus* was found (Rees, 1977). Thus, intraspecific competition probably limited the maximum numbers of larvae that matured per head in Montana, USA.

Feeding by *R. conicus* on North American species of *Cirsium* was first reported during this period. In Ontario, Canada, Laing and Heels (1978) reported the use of both introduced *Cirsium* species (*C. vulgare, C. arvense*) and Maw (cited in Zwölfer and Harris, 1984) reported use of the native *Cirsium flodmanii* (Rydb.) Arthur, by weevils that were originally collected from *C. nutans*. In Montana, USA, Rees (1978) reported the use of the native *Cirsium undulatum* Spreng. (wavyleaf thistle), as well as two introduced *Cirsium* spp. (*C. arvense, C. vulgare*), by *R. conicus* shipped from Mulhouse, France, and Rome, Italy, for the control of *C. nutans*. Rees (1978) found that 41% of the 517 wavyleaf (*C. undulatum*) thistles examined had *R. conicus* eggs in 1976. Although larvae occurred in the heads of only 16% of the plants, 51% of the heads on those plants had one or more larvae. Similarly, heads on 47% of 9091 Canada thistle (*C. arvense*) stems sampled had *R. conicus* eggs, and 44% of the flowers on these stems had *R. conicus* larvae (Rees, 1977). Finally, 60% of 384 bull thistle (*C. vulgare*) plants had *R. conicus* eggs, and although only 18% of the *C. vulgare* plants had live larvae in their flowerheads, 47% of the heads on those plants were infested.

Unexpectedly, egg and first instar larval mortality on *C. nutans* were high in Montana, USA, 23.3–82.5% (Rees, 1977). However, late instar larval mortality was much higher within flowerheads of the *Cirsium* species than within heads of *C. nutans* in the Gallatin Valley. For example, among the larvae that developed enough to form larval cells, subsequent mortality was 41% on the native wavyleaf thistle (*C. undulatum*), versus 31% on Canada thistle (*C. arvense*) and 62% on bull thistle (*C. vulgare*), compared with less than 3% on musk thistle (Rees, 1977). Since both Canada and wavyleaf thistles reproduce vegetatively and bull thistle was not a preferred host, Rees (1977) suggested that: 'There is no evidence to date that *R. conicus* will suppress the other thistle species.' Subsequently, Rees (1978) concluded: 'Therefore, *R. conicus* will have little effect on their [*Cirsium* spp.] populations.'

In summary, based on their interpretation of the evidence available by the early 1980s, Zwölfer and Harris (1984) argued that a combination of four factors would provide strong selection pressure against major utilization of native *Cirsium* species in North America: (i) strong preference for *C. nutans* over *Cirsium* species, especially by the biotype imported from *C. nutans*; (ii) higher larval mortality on *Cirsium* species than on *Carduus* species; (iii) smaller adult size, and so presumably lower fecundity, on *Cirsium* species than on *Carduus* species; and (iv) low population densities of the North American *Cirsium* species would not be sufficient to support *R. conicus* population development. Thus, although the data available did not provide strong, unequivocal support for these postulated differences and feeding on native *Cirsium* species had already been reported, they concluded that despite some concern at the time (1984) it was unlikely that *R. conicus* would have an impact on North American *Cirsium* species.

Recent studies of *Rhinocyllus* (1986–1999)

Variation in phenology

In North America, recent work supports the hypothesis of latitudinal variation in activity and development of *R. conicus.* For example, in Virginia the activity of overwintered adult weevils was observed to start in mid to late April in Virginia, USA (http://www.nysaes.cornell.edu/ent/biocontrol/weedfeeders/rhinocyllus_c.html) and in Nebraska on 13 May in 1998 (S.M. Louda, unpublished results). Also, newly developed teneral adults were observed in Colorado, USA, in June and July (http://www.ag.state.co.us/DPI/publications/muskthistle.html). However, further north in south-central Alberta, Canada, overwintered adults appeared only in early June and newly emerged adults were seen in August (A.S. McClay, Alberta, 1999, personal communication). Thus, geographical differences in activity pattern can have an environmental component. Furthermore, in Europe, Aeschlimann (1999) confirmed Zwölfer's (1967) observation that the activity period of the *R. conicus* in the more southern Mediterranean climatic region was earlier than that in the more temperate climatic area of Europe. He found that the adults of *R. conicus* in the Mediterranean climate of Montpellier in southern France were active in early spring, and that their progeny started to emerge as adults in the second half of June. Alternatively, the adults of *R. conicus* in the Atlantic climate of Dordogne in south-western France were observed ovipositing later, mainly in early summer, and the new adult progeny started to emerge in mid-July. These results reinforced the suggestion of geographical intraspecific differences in *R. conicus* phenology.

Phenotypic and genetic variation in host use

In Germany, Klein (1986) studied host selection of *R. conicus,* and he concluded that the sequence in which *R. conicus* would exploit *Carduus* and *Cirsium* species within a site was predictable, using plant phenology and flowerhead availability. The earlier flowering species tended to be used first within each site. At Südpfalz, *R. conicus* used *Cirsium palustre* first, and then *C. arvense.* Near Bad Dürkheim, *R. conicus* used *Carduss nutans* first and then

C. acanthoides. In a third study site, *c.* 20 km north of Bad Dürkheim, *R. conicus* used *C. acanthoides, C. arvense, C. crispus* and then *C. vulgare* (Klein, 1986). Subsequently, Zwölfer (1988) questioned the widespread use of the biotype concept, e.g. by Zwölfer and Preiss (1983). Instead, he proposed that *R. conicus* use of *C. vulgare* in south-western France was more likely due to flowering synchrony rather than to an innate preference for *C. vulgare* over *C. nutans.*

In California, Goeden and colleagues pursued their long-term study of variation in *R. conicus* (Goeden *et al.*, 1985; Unruh and Goeden, 1987). Their studies originally suggested a mismatch between host plant and weevil biotype as an explanation for the initial failure of *R. conicus* to establish on *S. marianum* in California (Hawkes *et al.*, 1972; Goeden, 1978). Allozyme data were consistent with some degree of genetic differentiation of *R. conicus* from milk thistle (*S. marianum*) from *R. conicus* from musk (*C. nutans*) and Italian (*C. pycnocephalus*) thistles. Although only one locus (of five) showed a fixed genetic difference, allelic frequencies at the four other loci differed significantly among weevils from milk, musk and Italian thistles (Unruh and Goeden, 1987). However, Goeden *et al.* (1985) also found that *R. conicus* from *C. pycnocephalus* did oviposit on *S. marianum,* 6 years after its initial colonization of *C. pycnocephalus* when the flowerheads were nearly saturated with weevil eggs. Interestingly, the *R. conicus* from *S. marianum* began ovipositing on *C. pycnocephalus* quickly, only 1 year after its establishment, and it slowly increased its rate of oviposition on *C. pycnocephalus* over the next decade. Thus, genetic variation occurred among populations of *R. conicus.* However, the role of that variation in host use by *R. conicus* remained incompletely understood.

In Europe, Klein and colleagues performed a comprehensive allozyme and morphometric analysis of 14 widespread populations of *R. conicus,* collected from France to Israel. They showed that the populations divided into two well-differentiated, concordant groups on both sets of criteria (Klein, 1991; Klein and Seitz, 1994). The groups segregated into a north temperate group and a more southern, Mediterranean climate group, dividing at about the same latitude as the northern distribution border of the cultivated olive tree (Klein and Seitz, 1994). The *R. conicus* adults of the Mediterranean group had a narrower body, a 4 week earlier activity period, and a shorter oviposition period than did those of the temperate group. These traits – smaller size, plus earlier and shorter oviposition period – could be adaptations related to use of *Silybum* species. Klein and Seitz (1994) suggested that the two groups represented subspecies, and they proposed that the Mediterranean subspecies was equivalent to the taxon previously described as *Rhinocyllus oblongus* Cap. In summary, the evidence now suggests that differences in host use or preference between the two groups (subspecies) of weevils may have a genetic component, whereas differences in host use within each subspecies of *R. conicus* are probably related to temporal availability of flowerheads (Klein, 1986, 1991).

The temperate *R. conicus* group has been divided further by Briese (1996), into oceanic-climate and continental-climate types. He found that *R. conicus* attacked *C. pycnocephalus* in southern France mainly after *S. marianum* had finished flowering, whereas *R. conicus* from further north were associated instead with *Carduus* and *Cirsium* species. Relative use shifted east to west, from primarily *Carduus* species in the east to primarily *Cirsium* species in the west. The types also differed in pattern of activity and showed some genetic differentiation, although not as much as between the temperate and Mediterranean groups (Briese, 1996). The oceanic-climate type, which has a long pre-oviposition period after hibernation, was more closely associated with *Cirsium* species than with *Carduus* species. The long pre-oviposition feeding period would increase the coincidence of the *R. conicus* oviposition period with later flowering *Cirsium* species, like *C. vulgare*, near the Atlantic coast in France. The continental-climate type, which has a short pre-oviposition period after hibernation, was more closely associated with earlier flowering *Carduus* species than with *Cirsium* species, although some use of *Cirsium* species was observed (Zwölfer, 1967; Briese, 1996). Thus, recent research on both continents suggests that host use reflects both a hierarchy of innate host preference and the degree of synchrony between flowering and oviposition periods, with the synchrony influenced by physical conditions.

Non-target feeding on *Cirsium* species in North America

Data presented in 1985, plus work in progress at the time, raised again the issue of non-target effects in the biological control of weeds (Andres, 1985; Turner, 1985). Documented reports of feeding by *R. conicus* on native North American *Cirsium* species were published shortly after by Goeden and Ricker (1986a,b, 1987a,b) and Turner *et al.* (1987). These studies detailed the development of *R. conicus* within the flowerheads of at least 17 native *Cirsium* species in California, USA. For two of the native California species (*Cirsium californicum* Gray, *Cirsium proteanum* J.T. Howell), Unruh and Goeden (1987) used electrophoretic evidence to suggest that *R. conicus* had transferred on to them from *Carduus pycnocephalus*, rather than from *C. nutans.*

These pioneering studies of *R. conicus* on non-target native species are important, since they presage some of the recent findings in the Great Plains. For example, in samples taken in 1983–1985, Turner *et al.* (1987) found *R. conicus* in 57% of the native California *Cirsium* species sampled, representing four of the five sections of *Cirsium* native to America north of Mexico (Ownbey *et al.*, 1975). Furthermore, they were the first to record that three rare California *Cirsium* species were readily used by the weevil. In the light of these findings, they stated ‘This extension of its host range is not surprising because European *Cirsium* was known to be within the host range of *R. conicus*'. Surprisingly, they also found that the weevils from non-target *Cirsium* hosts were significantly larger than those from target *Carduus* hosts. Finally, Turner *et al.* (1987) pointed out that *R. conicus* was successful on native *Cirsium* species, and this contradicted the prevalent idea that native host-specialist insects would competitively exclude introduced biological control insects with a similar trophic niche (e.g. Peschken, 1984).

To date, *R. conicus* has been reared from flowerheads of native *Cirsium* species in every extensive survey of native *Cirsium* species in the USA: in California (Goeden and Ricker, 1986a,b, 1987a,b; Turner *et al.*, 1987; Turner and Herr, 1996; Palmisano and Fox, 1997), in Colorado (Louda *et al.*, 1997), in Montana (Rees, 1977, 1991), in Nebraska (Louda *et al.*, 1997; Louda, 1998), as well as South Dakota and Wyoming (Louda *et al.*, 1997). Because of ongoing studies of thistle–insect interactions in prairie grasslands, Louda and colleagues were the first to be able to quantify: (i) the population dynamics of host range expansion by *R. conicus* (Louda, 1998, 2000a); (ii) the consequences of feeding by native floral insect herbivores on the population dynamics of a native thistle, *Cirsium canescens* Nutt., before the host range expansion of *R. conicus* (Louda *et al.*, 1990, 1992; Louda and Potvin, 1995); (iii) the demographic effects of accelerated seed loss caused by *R. conicus* for *C. canescens* after the expansion (Louda *et al.*, 1997; Louda, 2000a; Louda and Arnett, 2000); and (iv) the indirect effects of *R. conicus* on native inflorescence insects (Louda *et al.*, 1997; Louda and Arnett, 2000; and unpublished data). The evidence from these studies on the ecological effects of *R. conicus* on native *Cirsium* species in prairies in the north-central USA is summarized below.

Thistle–insect interactions in prairies of the upper Great Plains

The ongoing studies of the floral herbivores in the population dynamics of native thistles in prairie grasslands were begun in 1976 (Lamp and McCarty, 1979, 1982a,b,c; Lamp, 1980). Four species of native *Cirsium* have been studied intensely so far: Platte thistle (*C. canescens*); its close relative, the federally listed threatened Pitcher's thistle (*Cirsium pitcheri* (Torr.) Torrey and Gray); wavyleaf thistle (*C. undulatum* (Nutt.) Spreng.); and tall thistle (*Cirsium altissimum* (L.) Spreng.). All four species are characteristic, short-lived perennial species in prairies. The local distribution of each of these native thistles is patchy (Great Plains Flora Association, 1986; Pavlovic *et al.*, 1992), and none is considered a serious weed (McCarty *et al.*, 1967).

A characteristic set of native insects feeds on or within the developing inflorescences of these thistles. On wavyleaf and Platte thistles in Sandhills prairie, the numerically most native important species damaging flowerheads are: two tephritid flies (*Paracantha culta* Wiedeman, *Orellia occidentale* [Snow]); three pyralid moths (*Homoeosoma impressale* Hulst., *Homoeosoma ardaloniphas* Goodson and Neunzig, *Pyrausta subsequalis plagialis* Haim:

G. Balogh, personal communication); and the adults of a curculionid weevil, *Baris subsimilis* Casey, whose larvae feed internally on stems and roots (Lamp, 1980; Louda and Potvin, 1995; S.M. Louda, unpublished data; C.W. O'Brien, personal communication). On Pitcher's thistle, the most common insects are the curculionid weevil (*B. subsimilis*) (C.W. O'Brien, personal communication) and two moths: the artichoke plume moth (*Platyptilia carduidactyla*; Pterophoridae) and *Homoeosoma* sp. nr. *impressale* (Pyralidae) (Louda and McEachern, 1995; and unpublished results).

In the prairie, insect herbivory on native thistles has been quantified for 25 years (Lamp and McCarty, 1979, 1981, 1982c; Louda and McEachern, 1995; Stanforth *et al.*, 1997; Jackson, 1998; Bevill *et al.*, 1999; Louda, 2000a; Louda and Arnett, 2000). These data show that feeding by native insects significantly reduces both flowerhead survival and subsequent seed reproduction by Platte, Pitcher's, tall and wavyleaf thistles. These studies have also been supplemented by experimental evaluation of the role of seed in the population dynamics of platte thistle (Louda *et al.*, 1990, 1992; Louda and Potvin, 1995), wavyleaf thistle in Nebraska sand prairie (Louda, 2000a; S.M. Louda, T. Tesar Huettner and J. Burger, unpublished results) and Pitcher's thistle in dune grasslands around Lake Michigan (Louda and McEachern, 1995; Bevill, 1998; Bevill *et al.*, 1999; and unpublished results). For Platte thistle, insect herbivores were crucial in limiting seed production, seedling establishment, local population density and lifetime fitness (Louda and Potvin, 1995). Seed availability can also limit the seedling establishment of wavyleaf and Pitcher's thistles. Thus, prior to the host range expansion by *R. conicus*, it was known that native inflorescence herbivores limited the seed production and subsequent population density of native thistles in dune grasslands (Louda *et al.*, 1990, 1992; Louda and McEachern, 1995; Louda and Potvin, 1995; Louda, 2000a; Louda and Arnett, 2000; S.M. Louda, unpublished data).

The first indication of the host range expansion by *R. conicus* on to Platte thistle and wavyleaf thistle at two long-term study sites, over 300 km apart in Nebraska sand prairie, occurred in 1993 (Louda *et al.*, 1997). Population growth of *R. conicus* since 1993 has been nearly exponential (Louda, 1998; 2000a). This host range expansion of *R. conicus* on to the two native *Cirsium* species occurred more than 20 years after the initial releases into Nebraska (1969–1974) of *R. conicus* from *C. nutans* from eastern France and north-central Italy. It is important to note that no *Carduus* species occur at the study sites in the Sandhills of Nebraska. The population growth of *R. conicus* in the Sandhills prairie nature preserves is consistent with the other evidence available on *R. conicus* use of the flowerheads of native thistles in the upper Great Plains (Louda *et al.*, 1997). Initial utilization of the native *Cirsium* species as hosts has been greatest on the early flowering species, and lowest on the high elevation (4150 m) species. Activity by *R. conicus* in Nebraska sand prairie is relatively early. Mating and oviposition by overwintered adults have been observed from mid-May to mid-June, with the new generations emerging from mid-July to mid-August (Louda, 1998).

The initial increase of *R. conicus* in the Sandhills of Nebraska has been most significant for seed production and population demography of the earlier flowering species, Platte thistle (*C. canescens*) (Louda, 2000b). Louda (1998) hypothesized that synchrony of flowering with the period of *R. conicus* oviposition activity helped to explain this difference in initial susceptibility to *R. conicus* between the co-occurring native species, *C. canescens* and *C. undulatum*. The average number of viable seeds produced by flowerheads of Platte thistle infested with weevils in 1996 was 14.1% of that produced by similar heads with no insects or only native insects (Louda *et al.*, 1997, 1998). The weevil increased the number of seeds lost to all insects, both per head and per plant (Louda, 2000a). Since the recruitment, density and fitness of Platte thistle were previously shown to be proportional to the number of viable seeds (Louda and Potvin, 1995), the added fivefold reduction in seed imposed by *R. conicus* leads to the prediction of a severe, potentially fivefold, reduction in plant population density of this already sparse native species. Data from demography plots (1990–1999) are consistent with this prediction (Louda, 2000a; Louda and Arnett, 2000). Finally, the striking, well-documented parallels between Platte thistle and its rare congener, Pitcher's thistle (*C. pitcheri* [Torr.] Torrey and Gray) (Louda, 1994; McEachern *et al.*, 1994; Louda and McEachern, 1995; Bevill *et al.*, 1999), suggest that the same thing could happen to Pitcher's thistle if *R. conicus* were to become established in the dune ecosystem around the Great Lakes (Louda *et al.*, 1997, 1998).

Additionally, the experimental evidence now provides support for the hypothesis of indirect ecological effects of *R. conicus* on the native inflorescence insects. These insects exploit flowerheads of the same stage and size as those used by *R. conicus* (Mellini, 1951; Harris and Zwölfer, 1971; Lamp and McCarty, 1982a,c; Zwölfer and Preiss, 1983; Zwölfer and Harris, 1984). A dramatic drop in the numbers of the early tephritid, *Paracantha culta*, in Platte thistle (*C. canescens*) flowerheads was correlated with the sharp increase in the numbers of *R. conicus* from 1994 to 1996 (Louda, 1998, 2000a). In a recent experimental test, the number of *P. culta* reared per head increased dramatically when the *R. conicus* eggs were removed by hand, compared with both control flowerheads and flowerheads on which *R. conicus* eggs were experimentally augmented (Louda, 2000a; Louda and Arnett, 2000; and unpublished data).

In summary, post-release ecological studies of the use of native thistles by *R. conicus* show five main patterns: (i) occurrence is geographically widespread (Goeden and Ricker, 1986a,b; Turner *et al.*, 1987; Turner and Herr, 1996; Louda *et al.*, 1997; Palmisano and Fox, 1997); (ii) levels of use of native thistles in the central USA are high and increasing (Louda *et al.*, 1997, 1998); (iii) exponential population growth on native thistles in Nebraska showed a long (i.e. more than 20 years) lag after introduction

(Louda, 1998); (iv) both direct and indirect effects occurred; and (v) the greatest obvious impact so far has been on a species that is monocarpic, phenologically synchronized with *R. conicus*, characterized by a short flowering period, and limited in population density by seed availability. Louda and colleagues (Louda *et al.*, 1997, 1998; Louda, 2000a,b; Louda and Arnett, 2000) have argued that, although the occurrence of some feeding by *R. conicus* on North American *Cirsium* was considered likely (Zwölfer and Harris, 1984), neither the amount of that feeding nor the size of the ecological effects associated with this feeding were predictable from the data taken in pre- and early post-release studies.

Altered ecological interactions in the new environment?

One prerequisite for success in the biological control of weeds, and that may lead to unexpected pressure on non-target plant hosts in a new environment, is that the herbivore population can reach high enough densities to reduce target host plant performance and density (Gassmann, 1996). The potential for such population growth is set by a species' innate demographic characteristics. These traits, in turn, are constrained by various ecological factors, such as interactions with natural enemies and resource competitors, as well as by host plant quality, climatic variability and habitat conditions. One possible explanation for the large non-target effects of *R. conicus* in North America is that the weevil was released from ecological constraints, such as imposed by its specialized natural enemies (Zwölfer and Harris, 1984) and by its adapted, inflorescence-feeding competitors (Zwölfer, 1978, 1988). In fact, based on the oviposition patterns of the weevil in Europe, Zwölfer (1971) thought that the selection of *R. conicus* for release in North America was 'fortunate', since high egg potential and a tendency to disperse its eggs should allow *R. conicus* to exert strong pressure on its host plant, after the weevil was released from limitation by its co-evolved competitors and parasitoids. Yet, these traits also contribute to high population growth rates and high densities, and so could increase the chance of both a spillover on to nearby native *Cirsium* species and dispersal movement into areas without its targeted (*Carduus* species) hosts. Although a greater diversity of parasitoids and predators on *R. conicus* is reported in North America than in Europe, the rates of parasitism were much lower in North America than in Europe (Zwölfer and Harris, 1984). Lower parasitism rates could allow the population build-up observed for *R. conicus* in North America, on both *Carduus* species in areas of deliberate introduction (e.g. Rees, 1977, 1982) and on *Cirsium* species in areas subsequently invaded (Louda, 1998). The role of these interactions in population growth and size of *R. conicus* merit further study.

In addition, interspecific competition with other co-evolved phytophagous insects, such as *Urophora solstitialis* and *Larinus sturnus*, within

C. nutans heads in Europe is a major cause of *R. conicus* mortality, and it probably contributes to limiting population growth there (Zwölfer, 1979; Zwölfer and Harris, 1984). Although native insects utilize the inflorescences of North American *Cirsium* species, interspecific competition could be lower in North America. The Nearctic inflorescence-feeding guild is simpler (Zwölfer, 1988), and in the upper Great Plains it lacks any native cleonine weevils (O'Brien and Wibmer, 1982). A decrease in guild competitive intensity could allow high population growth rates of *R. conicus* and lead to a spillover effect on to native *Cirsium* species. However, no data are yet available to document the occurrence of such a spillover effect.

Furthermore, there is conflicting evidence on the outcome of competition of *R. conicus* with tephritid flies. On *C. nutans* in Australia, Woodburn (1996) recently found *R. conicus* is unexpectedly out-competing *U. solstitialis*, the more effective biological control agent, even though *U. solstitialis* was thought to out-compete *R. conicus* in Europe (Zwölfer, 1979). On Platte thistle in Nebraska, *R. conicus* is outcompeting the native tephritid, *P. culta* (Louda and Arnett, 2000; and unpublished results). Unfortunately, no direct tests have been done on the interaction strengths and relative effects of competitors and predators on *R. conicus* population dynamics in either Europe or North America. *R. conicus* actually has natural enemies and significant potential competitors in the native inflorescence insects in North America as well as in Europe. Thus, these interactions need more evaluation, as does the hypothesis of more rapid population growth of *R. conicus*, with potential spillover on to *Cirsium* species, in North America.

One strategy for persistence in the face of a strong competitor is to 'spread the risk' by dispersing eggs widely. In Europe, at Mulhouse, France, 98.2% of the flowerheads of *C. nutans* were attacked by *R. conicus* in 1971, and the variance-to-mean ratio of eggs per *C. nutans* head was 0.70 (Zwölfer, 1971, 1979). As a result of predation and interspecific competition, the variance-to-mean ratio of the late larval/pupal distribution was higher (2.1–3.9) than that of eggs (Zwölfer, 1979). There was a highly significant negative correlation between the developmental success of *R. conicus* and the presence of *Urophora* and *Larinus* larvae (Zwölfer, 1979). Interestingly, the variance-to-mean ratio for its competitors suggested that they were more clumped; the variance-to-mean ratios were 9.6 for *U. solstitialis* (40.5% of the heads attacked), and 1.6 for *L. sturnus* (Zwölfer, 1971, 1979). In the United States, weevil aggregation was stronger than in Europe. In Montana, following the release of 2940 adult weevils at five sites between 1969 and 1973, the 'percentage of plants with eggs on flowers' increased from 88% in 1975 to 98% and 99% in 1976 and 1977, respectively (Rees, 1978). The variance-to-mean ratio of eggs per primary (terminal) flowerhead increased from 2.4 in 1975 to 37.9 in 1976, and 61.8 in 1977 (Rees, 1978). After egg and early larval instar mortality, the variance-to-mean ratio of third instar larvae in primary heads became even greater, going from 4.5 in 1975 to 5.1–5.8 in 1976 and 1997 (Rees, 1978), perhaps as a result of intraspecific competition. In Nebraska, Louda (1998) also reported strongly aggregated use of native thistles (*C. canescens, C. undulatum*) by adults of *R. conicus.* For example, between 1994 and 1996, the variance-to-mean ratio for adult *R. conicus* on Platte thistle (*C. canescens*) in May averaged 8.4 at Arapaho Prairie and 11.9 at the Niobrara Valley Preserve. Interestingly, the average variance-to-mean ratio for late larval/pupal number of *R. conicus* per Platte thistle plant, in the same period, increased substantially over that of the adult aggregation pattern, to 17.6 at Arapaho and 13.7 at Niobrara (S.M. Louda, unpublished data). In any case, although the data available for Europe and North America are not strictly comparable, they suggest that the distribution of the eggs and larvae of *R. conicus* on *C. nutans* tend to be more evenly dispersed in the indigenous region. Oviposition behaviour of *R. conicus*, which determines egg load distribution in Europe and North America, is also in need of further research to provide a better basis for predicting effectiveness.

Discussion

Our aim was to summarize the information available to provide a basis from which to address the general question of whether what was known, pre-release and early post-release, was sufficient to predict both the occurrence and the magnitude of impact by *R. conicus* on native thistles and their adapted floral insects. At least two main issues are confounded within the discussions over the risks associated with the deliberate introduction of exotic species for the control of exotic pest species. One issue is scientific: what evidence is required to evaluate the risks associated with various control methods, including those specific to classical biological control. The other issue is political, and can involve more rhetoric and hyperbole than fact. The evidence reviewed here can only be used to address the former issue. A review of such evidence in specific case histories is one way to learn from past mistakes in order to improve future efforts in biological control. Presumably such evidence will eventually be useful in a public context to resolve the political issue (Miller and Aplet, 1993).

Our first conclusion is that, in retrospect, the implications of the pre-release and early post-release data were that *R. conicus* would be likely to feed and develop upon some North American *Cirsium* species. The evidence suggesting the potential for problems appears to have been undervalued, reflecting both major reliance on field records to define the relative ranking among accepted hosts and the widespread acceptance of the idea of innate host preferences (biotypes) determining host-plant specificity. Our second conclusion, however, is that the studies needed to quantify the likely direct ecological consequences of that potential feeding on native species were not done, nor were studies done to examine the potential indirect effects of such feeding. Thus, in retrospect, more tests were required to complete the assessment of the ecological implications of the documented diet breadth. It is clear, however, that economic, not environmental, risks were the main focus of the scientific assessment of *R. conicus* for the biological control of thistles. The rationale for our conclusions reflects the information presented above and the following assessment of it.

Host specificity: feeding acceptance, oviposition and larval performance

The most consistent criteria used for the evaluation of potential non-target feeding are measures of insect host specificity or diet breadth (McEvoy, 1996). Generally, these measures include: (i) feeding acceptance when starved; (ii) feeding preference when given a choice; (iii) oviposition (under choice and no-choice conditions); and (iv) subsequent larval performance on a range of related and unrelated potential host plants. Feeding tests of *R. conicus* on leaf material, both starvation (= no-choice) and preference (= choice) evaluations, were done early in the programme. In the starvation tests of *R. conicus* from *C. nutans*, the form introduced into most areas of North America including Nebraska, the intensity of feeding on most *Cirsium* species as well as weevil survival on *C. undulatum* were lower than that on *C. nutans*. However, it was clear that some *Cirsium* species were accepted, including the one North American native species that was tested, *C. undulatum* (Zwölfer, 1964, 1967; Zwölfer and Harris, 1984). In the feeding preference tests of *R. conicus* from *C. nutans* carried out by Zwölfer (1964, 1967) and summarized by Zwölfer and Harris (1984), no consistent preference was detected for *Carduus* species over *Cirsium* species (Zwölfer, 1964). Despite this, the patterns in the field, plus the conviction that *R. conicus* was divided into host-specific races, led to the interpretation that feeding on native *Cirsium* would be slight (Zwölfer and Harris, 1984).

Oviposition and subsequent larval performance were also at least partially evaluated. First, field data on host use suggested a strong association with the targeted weeds. Second, egg deposition while feeding on leaves in no-choice tests was recorded, but the meaning of such data is ambiguous. Third, the no-choice oviposition tests done in field cages with four European species (two *Carduus* spp., two *Cirsium* spp.) showed that both *Carduus* and *Cirsium* species would support complete larval development (Zwölfer, 1967; Zwölfer and Harris, 1984). The field associations received more emphasis than did the garden oviposition tests. However, although the early field data suggested that *R. conicus* generally had a strong preference for *C. nutans* over *Cirsium* species, the realized pattern of use in the field was also influenced by environmental conditions and biotic interactions as well as innate preferences. Further, the laboratory tests did not substantiate a clear preference for *Carduus* over *Cirsium per se*, but suggested a preference among species within each genus. Today, such results would be viewed as evidence that further, larger-scale tests were warranted to quantify the factors determining the patterns and the variation in feeding impact and insect performance (relative adult survival, female oviposition, larval survival). Further choice and no-choice oviposition tests, including native North American species, to quantify relative egg loads among acceptable species, would have helped to calibrate the relative risk to *Cirsium* vs. *Carduus* species. Recently, Arnett and Louda (unpublished data) found that *R. conicus* from Nebraska still exhibited feeding and oviposition preferences for *C. nutans* over the native *C. canescens*, but also showed significant levels of acceptance of *C. canescens* even in the presence of *C. nutans.* Added no-choice oviposition and larval development tests with synchronously flowering native North American *Cirsium* species, such as *C. canescens* (Platte thistle), would also have improved quantification of the direct ecological risk to natives at low densities or in the absence of the targeted host plant. Such tests should be done as background for contemporary biological control decisions.

Given Zwölfer's (1967) early suggestion that flowering phenology probably influenced host use by *R. conicus* in the field in temperate Europe, we wonder about the real meaning of the evidence on feeding and oviposition preference. To what extent could the evidence on preference reflect environmental differences – the result of experience, physical conditions or ecological context – rather than innate, heritable differences? The data in the unpublished early reports (e.g. Zwölfer, 1964, 1967) suggested that the innate preference of *R. conicus* is likely to be only a partial predictor of host use in the field. Based on his field observations, Zwölfer (1967) suggested that a possible explanation for the variation in the use of *C. vulgare* in Italy and France 'may be found in the different phenology of the weevil populations . . . The upper Rhine Valley populations of *R. conicus* start their activity very early and are better synchronized with *C. nutans* than with *C. vulgare*, whilst the contrary may be the case with the Apennines populations.' Genetic variation exists among populations of *R. conicus* in Europe and those introduced into California (Goeden, 1978; Goeden *et al.*, 1985; Unruh and Goeden, 1987; Klein, 1991; Klein and Seitz, 1994; Briese, 1996). However, genetically determined host plant specialization is not sufficient to explain either the patterns of variation in host choice or geographical variation in that choice within the indigenous region.

Even though an ecological factor (flowering phenology) was initially suspected to be a critical parameter for predicting host use in the field, no further studies of ecological factors were performed. Instead, the reliance on patterns in the field survey and on evidence of some genetic variation, plus the inference that such variation contributed significantly to host specificity, were widely accepted (e.g. Zwölfer and Preiss, 1983; Zwölfer and Harris, 1984). In retrospect, this was unfortunate. The wide geographical range, and evidence of the associated broad ecological tolerance of *R. conicus* across Europe, as well as the feeding breadth within the Subtribe *Carduinae*, which contained native North American species, should have stimulated further studies of the ecological parameters involved in the host choice, reproductive success and population growth of *R. conicus.*

Host specificity: larval survival and performance

The second part of most evaluations of the potential risk of non-target use involves evaluating insect host specificity by larval performance on the range of accepted potential host plants. Larval performance is generally defined by survival, development time and subsequent adult size. Lack of complete development in a well-designed test is reasonable evidence that immediate ecological effects are unlikely, although it does not preclude strong selection for adaptation under the right circumstances over the longer run (Secord and Kareiva, 1996). Slower rates of larval development have been interpreted as evidence of low impact potential (Zwölfer and Harris, 1984). However, this case history demonstrates that such evidence can underestimate the eventual use and ecological impact of the biological control agent on a less preferred non-target species (Louda *et al.*, 1997; Louda, 1998, 2000a; Louda and Arnett, 2000). With the pre-release tests in Europe and early post-release studies of *R. conicus*, for example, Zwölfer and Harris (1984) inferred that larval survival of *R. conicus* was higher, development was faster, and subsequent adults were larger on *C. nutans* than on *Cirsium* species. Thus, they concluded that 'a combination of the preference of the *C. nutans* strain of the weevil for its own host species, a high [larval] mortality and presumably low fecundity resulting from small size when reared on other thistles implies a strong selection pressure against their [*Cirsium* spp.] utilization.' They also argued that 'to overcome the negative selection pressures of adult oviposition preferences and high larval mortality, the thistle involved should be abundant. Thus it is unlikely that the normally scattered native thistles will be adopted as a prime host.'

Unfortunately, this has not turned out to be the case. Feeding and oviposition preferences were not relevant when *Cirsium* species occurred without *Carduus* species (Louda, 1998; Arnett and Louda, unpublished data). Development of larvae into adults on Flodman's thistle (*C. flodmanii*) in Canada (Maw, cited in Zwölfer and Harris, 1984), and on Platte (*C. canescens*) and wavyleaf (*C. undulatum*) thistles in Nebraska (Louda, 1998; Arnett and Louda, unpublished data) was high, though not as high as on *Carduus* species. In fact, in Nebraska, we know that larval survival and development were sufficient to lead to explosive population growth (Louda, 1998). So, the population growth and impact of *R. conicus* on Platte and wavyleaf thistles, specifically, has occurred in spite of lower larval survival and development on these species. This suggests that we should 'believe our data' (Louda, 2000a) and pursue contradictions and conflicting data if they emerge in early tests.

In summary, the preference and performance data from pre-release studies and early post-release studies suggested that some *Cirsium* species were acceptable host plants, and that development could be completed on them. Since differences in rates of acceptance and development were considered significant, and the economic imperative was primary, none of the further testing suggested by the data was undertaken. Contemporary concerns over environmental risk should make such tests standard now.

Prediction of quantitative ecological effects

Given that the preference and performance data actually did show that *R. conicus* would feed and develop on some *Cirsium* species in Europe, and so would be likely to use some *Cirsium* species in North America, were the observed population build-up and numerical impact of the weevil on the non-target North American thistles predictable? Moreover, were the indirect negative impacts on the associated native floral insects predictable? In the context of the usual contemporary testing protocols, to what extent did the standard preference and performance tests predict the ecological effects of *R. conicus* now documented? Are preference and performance tests sufficient to predict what 'intermittent feeding' under test conditions portends under new environmental conditions? The review of the data suggests that preference and performance, as evaluated in this case, were necessary but not quite sufficient to predict the numerical effects of *R. conicus* on less preferred host species under field conditions. Three types of evidence support this interpretation.

Firstly, actual testing of native North American species was clearly not a high priority of the biological control programmes before 1985, with the *Euphorbia esula* L. programme being a notable exception in North America (Pemberton, 1985a). For *R. conicus*, none of the pre-release choice tests included native North American species (Zwölfer, 1967; Zwölfer and Harris, 1984). Only two of the early post-release studies looked for development of *R. conicus* on native North American *Cirsium* species; one unpublished study in Canada on *C. flodmanii* (Maw, cited in Zwölfer and Harris, 1984) and one in Montana on *C. undulatum* (Rees, 1978). These results for native species contrast with the much more extensive evaluation of economic plant species (Zwölfer, 1964, 1967, 1969; Zwölfer and Harris, 1984).

Secondly, without evaluating the mechanisms leading to relative egg loads under field conditions in Europe, the quantitative use of various *Cirsium* species in North America could not be predicted. Observed patterns of utilization are influenced by environmental differences, and laboratory patterns of preference may or may not predict the relative amount of use among acceptable species under variable field conditions. In addition, no studies were carried out to quantify the consequences of feeding on the less preferred populations of potential host plant species within the main regions of study, either in Europe or in North America. Such tests are required to provide some insights into the potential quantitative impact of feeding, when the preferred host is unavailable or when ecological conditions in the field shift the spectrum of host resources available. Such field data, in addition to the adult preference tests and subsequent larval performance tests, would probably have identified the potential magnitude of the non-target feeding impact of *R. conicus* on early flowering native North American *Cirsium* species that occur within the altitudinal range of the weevil.

Thirdly, comparative studies of the reproductive biology and life tables of *Rhinocyllus* 'biotypes' on non-target key species could have been used to test the hypothesis of population build-up by each 'biotype' under new environmental conditions. Comparative studies in Europe and North America of the flowerhead guild of thistle species, with and without *Rhinocyllus,* could have helped in understanding the role of horizontal effects, such as competition interference and cannibalism, on *Rhinocyllus* dynamics as well as the indirect impacts on other insects.

Thus, further studies of variable host plant use in Europe should have been used to determine the relative risk to *Cirsium* species under different environmental conditions, and to evaluate Zwölfer's (1967) early inference that ecological context could be critical. These studies could have quantified egg loads and larval success rates on less preferred plant host species, such as some *Cirsium* species, both near to and removed from the vicinity of a more preferred *Carduus* species of host plants. Similarly, these parameters could also have been tested under different physical conditions, such as those that affect phenology. Post-release comparative and experimental studies of feeding and oviposition on potentially acceptable North American *Cirsium* species were, and continue to be, merited for potentially vulnerable and rare species and for those whose flowering phenology coincides with the oviposition period of *R. conicus.* The type of studies needed could be designed on the model of the recent field assessment of the quantitative role of floral herbivores in the population density and dynamics of *C. nutans* in France (Sheppard *et al.*, 1990, 1994) or in New Zealand (Shea and Kelly, 1998), if they were extended to evaluate impacts on other acceptable species besides the one targeted for control.

Conclusions

Our review of the evidence on *R. conicus* and its relevance for resolving the controversy over the data available was required to assess the risk of deliberate introductions for the biological control of weeds, such as true thistles, and it leads to three conclusions.

First, in retrospect, the pre-release plus the early post-release data did suggest that *R. conicus* would be likely to feed, and could develop, on multiple *Cirsium* species, including important clues that North American species would be among these species. However, several factors influencing the programme at the time led the investigators to discount this evidence. These factors were: (i) a widespread acceptance of the host race paradigm; (ii) a focus on preventing damage to economic plants, which entailed selecting test plants for the screening tests which were almost exclusively cultivated plants; and (iii) a strong desire to move quickly to eliminate the weed problem. These factors contributed to a de-emphasis on the data that showed significant feeding, oviposition and development on some European and a couple of North American *Cirsium* species. A strong emphasis was placed, instead, on why the evidence was not sufficient to predict a major effect by *R. conicus* on native plant species. This latter emphasis precluded further studies, to examine conflicting data and to determine the ecological factors influencing host selection in the field.

Second, again in retrospect, the studies needed to quantify the likely magnitude of feeding and development by *R. conicus* on *Cirsium* species, and thus the ecological consequences of that feeding, were not done in this case, nor in any other up to that time as far as we are aware. Thus, a clear prediction of the intensity of direct effects, and of the type and magnitude of indirect ecological effects resulting from the feeding and potential development, was not possible. However, the early data did provide reasons to hypothesize that ecological effects might occur if *R. conicus* did include North American *Cirsium* species in its list of acceptable, phenologically exploitable host plants. For example, starvation feeding tests showed ‘regular and spontaneous feeding’ by *R. conicus* on at least two European *Cirsium* spp. (*C. arvense*, *C. vulgare*), and preference feeding tests showed higher acceptance of European *Cirsium acaule* than of *Carduus nutans*. Furthermore, larval development was also completed on European *Cirsium arvense* and *C. palustre*.

Third, the findings imply the potential for a direct, negative effect by *R. conicus* on fitness and seed production of *Cirsium* species when exploited. Interactions with other insects in the floral herbivore guild were noted, implying the potential for indirect interactions with insects in the North American inflorescence guild. However, these clues in the observations and data from pre-release and early post-release studies were not pursued. Some of the information needed could have been developed through quantitative field studies of relative egg loads on alternative hosts, under a range of environmental conditions within the geographical range of *R. conicus* in Europe. Such data would quantify the potential variation in magnitude of use of less preferred, but acceptable, host plant species. Thus, we conclude that more information could have been acquired to assess the ecological consequences and potential control effectiveness, and these data are now required under contemporary conditions.

In summary, we conclude that there were enough data suggesting that *Cirsium* species were acceptable host species to have aroused more suspicion over the potential consequences of introducing and redistributing *R. conicus* in North America without further testing. However, accurate prediction of the observed quantitative ecological effects would have required more field and laboratory experiments. Contemporary concerns now mandate such additional, pre-release testing.

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9

Risk Analysis and Weed Biological Control

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Abstract

Weed biological control and risk analysis are very powerful tools for land management and decision-making respectively. We explore the application of risk analysis to weed biological control. Recent criticisms of weed biological control have mainly centred on non-target impacts, attacks by the biological control agent on species other than the weed. In ecology, these are *direct effects* because they involve physical interactions between the species concerned. *Indirect effects* are those in which the species do not physically interact. In biological control terms, indirect effects include, on the positive side, the increase in pasture production or biodiversity resulting from successful biological control. On the negative side, they include the decline of a native species that had used the weed as habitat. The aim of weed biological control is then to maximize the ratio of desirable indirect effects to undesirable direct and indirect effects. Using a risk analysis approach, we show that the problems of weed biological control are less in the domain of science and more in that of communication and consultation. A well-conceived biological control project would aim for wide consultation to agree on the target weed with the community, so that negative effects are viewed as trivial against the positive ones. It would also use highly specific agents to reduce the risk of undesirable direct effects to a minimum. Lastly, 'biocontrollers' themselves would merely be advisers on the decision to release.

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Introduction

Classical biological control of weeds is an extraordinarily powerful tool for vegetation management. Risk analysis is a tool for making decisions and handling risks. This chapter is about combining these tools to maximize the desirable and minimize the undesirable effects of weed biological control. To be successful, weed biological control has to have a substantial direct impact on the target weed. We define *direct effects* here as the effects of feeding or damage on the target weed or on any non-target species by the biological control agent. Direct effects may be at the level of the individual plant or at the level of the population; the point is that they are the effects on the species that the agent feeds on, or that feed on the agent.

Such direct effects will have a number of indirect consequences for other components of the ecosystem. *Indirect effects* occur when other species, not directly attacked by the agent, are affected by the agent's abundance or by its feeding on a species (Fig. 9.1). The destruction of a dense, shading, environmental weed will allow the resurgence of the native ground flora, for example, while that of a cropping weed will allow crop yields to increase. This is why we are controlling the weed in the first place. In fact, indirect effects – desirable ones – are what we are trying to achieve by controlling the weed. It would be an ill-conceived project in which the control of the weed were an end in itself. This pair of definitions for direct and indirect effects is logical and in keeping with the wider ecological literature (see Wootton, 1994). The relationship between kinds of direct and indirect effects is more clearly shown in Table 9.1. 'Case 1' effects, direct and desirable, are the simplest; the agent controls the target weed. 'Case 2' effects are undesirable direct effects, where the agent attacks a non-target plant. Much of the recent controversy in biological control has centred on this type of effect (e.g. Louda *et al.*, 1997). 'Case 3' and 'Case 4'

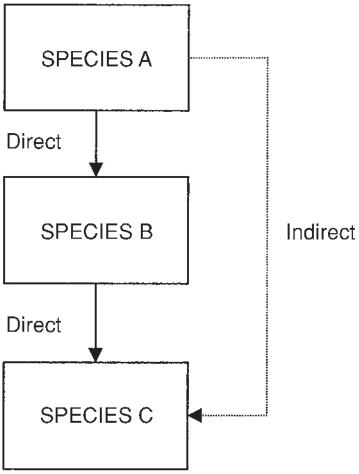

Fig. 9.1. The relationship between direct and indirect effects in ecology. Arrows show the interactions between species. As a result of grazing by insect species A, plant species B becomes scarce (direct effect of A on B), driving down populations of species C which feeds upon it (direct effect of B on C, but indirect effect of A on C). If A were a biological control agent and B were a weed, society would probably accept the indirect effect on C as a necessary evil. If, on the other hand, B were a native plant, and C a rare native insect reliant on it, we would have a problem: both the direct non-target effect of A on B and the indirect effect of A on C would be undesirable (see also 'Risk communication').

Table 9.1. Possible types of effects resulting from biological control of weeds. Much of the recent controversy in biological control of weeds has centred on undesirable, direct effects (i.e. Case 2).

Type of effect of biological control agent	Desirable	Undesirable
Direct	Case 1 Example: agent feeds on target weed, reducing its abundance	Case 2 Example: agent feeds on non-target species
Indirect	Case 3 Example: control of weed allows regrowth of native vegetation or useful pasture	Case 4 Examples: control of weed results in expansion of new weed; control of weed causes loss of habitat for native wildlife

effects are the indirect effects resulting from the activities of the agent. Consider the following scenario: the agent causes a decline in the competitive ability of the weed (Case 1), which results in reduced abundance. The consequent increased abundance of pasture species (Case 3) leads to an increase in wool or meat off-take (Case 3). On the other hand, the 'Case 1' effect described also reduces abundance of a native animal that had relied on the weed for sustenance (Case 4). In general, the outcome of any successful weed biological control project would be a series of major 'Case 3' effects (e.g. higher production, lower herbicide inputs, higher profitability, enhanced biodiversity, etc.), with minimal Case 4 effects.

Risk analysis and biological control: some definitions

Not every environmental problem can be addressed, and priorities need to be set by agencies and land managers. In recognition of this, risk analysis has forced itself on to the agenda for governments around the world over the last 20 years. Biological control of course has used host specificity testing as a form of risk assessment (not strictly risk analysis, which is a broader term embracing risk assessment as one of its components – see below) for many years. However, the wider terminology and formulations of risk analysis have great power to generate insights. We present here a short introduction to the field.

Risk is the likelihood that damage can be caused; hazard is the agent that causes damage. When describing risk-based disciplines, risk analysis is the most general term, which comprises the following four components, referred to as the four pillars of risk analysis by Davies (1996a,b):

1. Comparative risk analysis consists of comparing two or more types of risk, principally a tool for policy-makers to decide on resource allocation.
2. Risk assessment is a set of analytical techniques for estimating how much damage or injury can be expected as a result of an event.
3. Risk management, in contrast to risk assessment, considers social, economic and political factors to determine the acceptability of damage and what action can be taken to mitigate it.
4. Risk communication is about conveying information about risk.

To these four terms we would add a fifth, monitoring, to detect the impact of hazards at an early stage (although purists might include such monitoring under the heading of risk management) or to provide data to refine future risk assessments. We will now expand on each of these terms in turn, as they apply to weed biological control, and will finish by synthesizing the insights for biological control from this rich field, in order to draw out strategies for the future.

Comparative risk analysis (CRA)

This has two forms. The first (also termed risk ranking) consists of comparing two types of risk. For biological control, this might be represented by Emberson's (1999) study of naturalized exotic insects in New Zealand: 97% were introduced accidentally and only 2.5% for biological control. Strictly, this does not give us the relative risks of accidental versus intentional introductions, as we cannot tell what proportion of accidental or biological control introductions become naturalized, but it does tell us that biological control is a small part of the overall invertebrate invasion story for New Zealand. This approach might involve comparing the risks of off-target effects of biological control with those of herbicidal control of the weed. The second type of CRA is of a larger scale. It is also known as programmatic CRA and is used for setting government priorities among a large number of risks. It involves more value judgements than risk ranking and is 'as much a philosophical as a scientific effort' (Davies, 1996b). Little of this sort has been attempted for weeds, though Australia's recent establishment (NWS, 1999) of a list of its top 20 weeds of national significance from among the 2200 or so (Hnatiuk, 1990) naturalized species is perhaps a limited example of this kind of approach.

Risk assessment

The NAS model

The term 'risk assessment' has been widely interpreted, particularly in the field of invasions, but has been formulated with great clarity by the National

Academy of Sciences (NAS, 1983). Theirs is the most generally accepted formulation (Davies, 1996b), consisting of a four-step process:

1. *Hazard identification* identifies the type of damage that can be caused. In our terms, this might include the feeding of an agent on a non-target plant, or the loss of habitat for an endangered bird which uses a weed as a nesting site. This is the area of risk assessment in which weed biological control is probably strongest. Much of the work on feeding trials falls into this category.
2. *Dose–response assessment* estimates the relationship between exposure to a harmful substance or event and the resultant harm caused. Not an easy thing to characterize for a herbivorous insect, there have nevertheless been a few published relationships (e.g. Figure 4 in Lonsdale and Farrell, 1998). However, in biological control this mostly consists of estimations of degree of damage based on the perceived impact from pre-release studies in quarantine or in the native range. This is generally on a discontinuous scale (if the insect attacks, what will be the result?) rather than on the continuous scale (what damage will a given density of insect cause?) implied by this methodology.
3. *Exposure assessment* estimates how much of a substance will reach a target population or how much of a population will receive some exposure to a substance. This is represented in weed biological control by climate modelling to assess risk to non-targets (see below).
4. *Risk characterization* combines information from steps 1, 2 and 3 to estimate the amount of damage that will be caused overall. In weed biological control, we largely rely on interpreting our host range work to carry out this stage.

Ecological models of risk assessment

Unfortunately, despite the admirable lucidity of the NAS model, which was developed largely for chemical pollutant risks to human health, it has to be modified for assessing the risk of ecological impacts (see also Simberloff and Alexander, 1994). This is because:

1. There is no stage identifying the species at risk; the NAS model was developed for risks to one species – humans – but in ecology, species vary hugely in their responses to different hazards.
2. In human health, we consider risks to individuals; in ecology, we may be concerned about impacts on individuals, on populations or on whole communities. For a rare species, one lost individual may be too much; for a common species, the population may be able to compensate for the loss of individuals up to a certain point. In ecological risk assessment, we must identify the level of organization at which the risk assessment needs to be carried out.

3. Biological control agents can reproduce and multiply, and potentially evolve, in stark contrast to chemical pollutants.
4. Human health risk assessors assume that there are no external feedback loops from the damaged to the undamaged portion of the population or ecosystem. In ecology, we must consider such interactions, especially where species are important determinants of community structure and function.

The risk assessment model of Lipton *et al.* (1996) builds on the NAS (1983) model to accommodate some of these objections. In this model, there are three additional stages, as well as modifications to the four original components of the NAS (1983) formulation (Table 9.2). The recent Environmental Risk Management Authority (ERMA) model, by which all introductions of new germplasm to New Zealand, including biological control agents, have to be assessed, also recognizes and addresses these objections (Anonymous, 1997). Clearly, this is a very involved process and it will be a rare biological control project that has sufficient resources to carry out this sort of analysis comprehensively. Nevertheless, by taking a systematic approach of this sort, even at a less detailed level, one may be able to identify potential problems very early in the project.

Difficulties of prediction

Implicit in the idea of risk analysis is the belief that we can predict the future from a knowledge of the past. This can be done in ecology, but within very broad bounds. The behaviour of ecological systems is inherently difficult to predict, particularly where exotic introductions are concerned (Williamson, 2000; Lonsdale and Smith, 2000). Here are some reasons why.

Performance in the native range

It is well known that phytophagous insects in the native range are often heavily parasitized, a fact that certainly would influence their population dynamics and perhaps even their behaviour. Thus simple measurements of the scale of the impact on particular species in the native range are a poor predictor of potential impact in the new range.

Explanation is not prediction

It is possible to explain ecological interactions much more easily than to predict them (see also Williamson, 2000). For example, the control of *Salvinia* by *Cyrtobagous* was explained by a simple model – perhaps the simplest imaginable in the circumstances – involving just five parameters to describe the interaction of the weevil and the plant (Lonsdale, 1996). Unfortunately, most of these parameters can only be measured *after* the introduction of the agent to its new range. Thus, the equation can be used

Table 9.2. The ecological risk assessment framework of Lipton *et al.* (1996), which builds on the NAS (1983) framework. Components additional to the original NAS (1983) framework are asterisked.

1 *_Receptor identification_. Here we characterize the biotic components and organization of the system, and the components most vulnerable to disturbance of the system. In biological control terms, this could involve drawing up a flow chart of the whole system under study, including target and non-target species, and higher trophic levels potentially affected

2 _Hazard identification_. Here one identifies hazards for the species listed in the receptor identification stage, and the system level (individual, population or community) at which those hazards will be expressed

3 *_Endpoint selection_. Here one chooses species and system levels that will be sensitive to the hazard, and relevant to ecological concerns. These will become the indicators that will be monitored. For a very rare non-target plant, one may decide to monitor all individuals to quantify any undesirable effect. For one that is less endangered, population-level monitoring may be acceptable, while damage to individuals may be compensated for by the rest of the population

4 *_Relationship assessment_. Using a knowledge of the ecology of the system, the presence of feedback loops to identify secondary and tertiary risks is evaluated. If new receptors are identified that may be affected by the biological control agent, it is necessary to repeat stages 2 and 3. Thus, stages 2–4 are an iterative process to identify the potential risks

5 _Response assessment_. The dose–response curve approach of the original NAS framework implies a level of data collection that is generally unavailable for the impact of one organism on another. Rather, in biological control one would perhaps explore the consequences of a low, medium or high density of the agent

6 _Exposure assessment_. Here we attempt to predict where the biological control agent will go, perhaps using climate modelling, and the extent to which it will overlap in space and time with the receptors

7 _Risk characterization/uncertainty analysis_. This last stage combines all the information above to evaluate and encapsulate the degree of risk posed to ecological end points. The stage is modified from the last stage of the NAS framework in that it also includes an analysis to identify uncertainties in each stage of the analysis, quantitatively if possible

only to explain the results of a past introduction, and not to predict the results of a new interaction involving another pair of species. The ability to predict indirect effects, given that the quantification even of direct interactions is so intractable, seems a long way off.

Idiosyncrasies and chance

The scoring systems of Harris (1973) and Goeden (1983) were developed to predict successful agents based on their biological attributes. A retrospective study by Boettcher and Lonsdale (1999) has recently shown that neither system would have been able to effectively screen agents that were subsequently found to be effective. Screening systems for biological control agents are usually based on heuristic rules rather than the mathematical symbols of the *Salvinia* example. They also often describe the past well, but not the future. This is because the success of an invasion is often the result of peculiarities of the interaction between the species and its new environment. Chance also plays a substantial part in invasion success; this is why establishment rates for exotics generally (e.g. Green, 1997) and for biological control agents in particular increase with release sizes and numbers (Memmott *et al.*, 1996).

Base-rate effect (prevalence) and the rate of false positives

Successful exotic pests and weeds – organisms that arrive in a new range, become established and then attain such abundance that they cause undesirable effects – are a comparatively small proportion of the species that actually arrive. Williamson and Fitter (1996) would suggest, as a broad rule of thumb, that only 10% of species pass each of the three sequential transition stages from introduced to pest status, giving an expected overall transition rate of 0.1% of the oncoming species that actually cause harm. The rates are highly variable, however, and factors influencing them are likely to include the following:

1. The degree to which species are pre-adapted to the climate of the new range (Williamson, 1996).
2. The degree to which species are helped through the very uncertain early establishment phase, especially by husbandry by other species such as man (e.g. Mack, 1996).
3. The number of propagules that arrives affects the establishment rate (e.g. Memmott *et al.*, 1996; Green, 1997; Lonsdale, 1999).

If we think of a biological control introduction as a form of planned invasion, with the impact on the target weed as cognate with the final ‘becoming a pest’ phase, we can see from these three factors that the likelihood of biological control agents having an impact is likely to be greater than the background 0.1% of introduced species. Biological control releases are not random introductions. Resources are directed towards matching the agents to the climate of the new range, nurturing them through the establishment phase, and ensuring that they are widely disseminated in large numbers across the range of the target weed. The results show that the rate of impact is consequently high: Williamson and Fitter (1996) show that 32% of introduced weed biological control agents have an impact on their target weed. This rate is two orders of magnitude higher than their background figure of 0.1% of all species that have an impact on other species following introduction to a new range.

How rare are undesirable effects in weed biological control? Despite the comparatively large proportion of biological control species that reach the stage of having an impact on the target weed, this does not mean that the probability of their having an undesirable impact is similarly elevated. If we introduce only host-specific agents (not always possible), the probability of a ‘Case 2’ (i.e. direct, undesirable) effect (Table 9.1) is infinitesimal (in Australia we know of no such effect resulting from host-specific agent shifting host, and it is thus impossible to calculate a probability). The probability of a ‘Case 4’ (i.e. indirect, undesirable) effect involves not a host shift, but an agent’s perturbing the system sufficiently that it causes cascade effects through the trophic levels or away from the site of impact on the target weed. As a first approximation, this might be assumed to result only from those agents that actually have a substantial impact on the target weed, as the abundance of the target weed is the mediator of their effect on the rest of the system. Thus, for host-specific or near-specific agents we are dealing with an unknown, but probably small, subset of those agents that directly impact on the target weed.

Our ability to predict an event depends on the general rarity of that event. This influence of rarity on predictive power is known as the base-rate effect (Matthews, 1996). The rate (in time or as a proportion of a population of events) at which an event occurs is called the base-rate or prevalence. The influence of base-rate on the reliability of screening systems has been much studied in the area of earthquake prediction (Matthews, 1997) and in medical epidemiology (Kraemer, 1992). Until recently, the application of the base-rate effect to the prediction of the negative impacts of introduced species has not been recognized, but, given the general rarity of such impacts, it has to be taken into account (Smith *et al.*, 1999). Briefly, when an undesirable event is generally rare, even an accurate screening system will produce a vast number of false positives that swamp the true positives, so that most predictions of harm will be wrong. Whether one then heeds the warnings of this system depends on the degree to which one fears the consequences of introducing a harmful species more than those of excluding a useful species. a choice that can be explored mathematically using decision theory (Smith *et al.*, 1999). For our purposes, it suffices to recognize here that for host-specific agents introduced into a new range, the probability of undesirable effects is probably low, and most of our predictions of harm will probably be wrong (Table 9.3, Fig. 9.2). Having surveyed the limitations of predictions of harm, let us turn to some predictive tools that have proved useful for biological control workers.

Prediction tools

Climate-matching

This is one of the oldest methods used; for example in the 1930s, the transfer of overseas surveys from England to southern France for potential *Hypericum* control agents led to improved success (see Briese, 1997). Climate-matching could also be used to determine whether a particular

Table 9.3. The base-rate effect as it applies to weed biological control species, assuming a screening system capable of winnowing out 80% of species that would cause harm to non-target organisms (e.g. Case 2 or Case 4 in Table 9.1) and a base-rate for such harmful effects of the order of 1% (= 10/1000). The rate of false positives (the proportion of harmless species among the rejected species) would be 198/206 = 96%, so a lot of potentially useful species would be discarded needlessly (see also Fig. 9.2 and Smith *et al.*, 1999). On the other hand, we would still be allowing in 80% of the species we started with. These proportions of course vary with base-rate (still little known) and with screening accuracy. Screening accuracy is very high for specificity (i.e. direct non-target effects), but is likely to be low for potential indirect effects.

	Harmful species	Harmless species	Total
Screened out	8	198	206
Allowed in	2	792	794
Total	10	990	1000

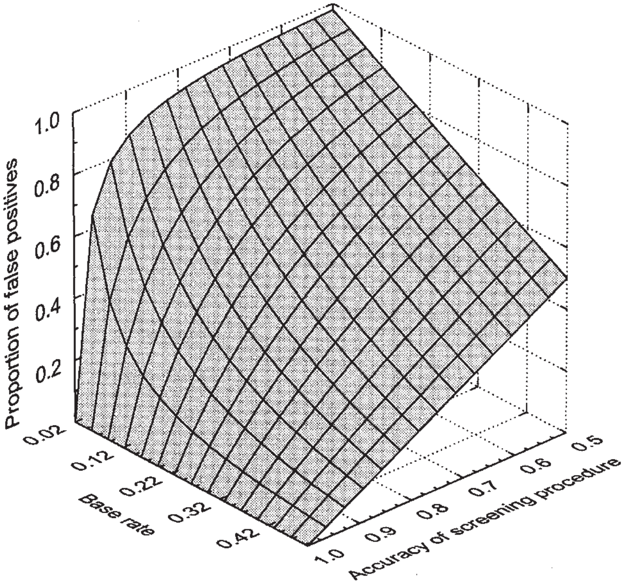

Fig. 9.2. The theoretical relationship between base-rate, screening accuracy and the proportion of false positive results (i.e. rejection of an agent that would not cause direct or indirect adverse effects following release) in a host-testing procedure (see also Smith *et al.*, 1999).

non-target plant is at risk to an agent, should it be found to form part of the agent's potential host range. Modern researchers are now able to use climate-matching models such as CLIMEX (Maywald and Sutherst, 1997). For example, Stewart *et al.* (1995) predicted the range of alligator weed and indicated where its control agent would be effective; Scott (1992) demonstrated why *Perapion* would not be useful on *Emex* in Australia; and Morin and Hill (1996) assessed the probability of successful rust establishment on mist flower in New Zealand. Not all predictions have been accurate, though, because localized responses to microclimate, phenology, host type, etc. all play a role in determining range (Samways *et al.*, 1999). However, as climate-matching models become more sophisticated, their reliability should increase.

Expert systems to select agents

The scoring systems mentioned above (e.g. Harris, 1973; Goeden, 1983) are very much centred on characteristics of the agents themselves, and are based on previous case studies of successful biological control. Expert systems (e.g. Cullen, 1995) are more forward-looking and force us to ask what we want of an agent in the particular case at hand. They are more dependent on ecological attributes of the target weed, and the identification of potential interactions between agent and host. All agent selection systems are more concerned with evaluating effectiveness than with safety. However, where potential risks are known well in advance, the framework of an expert system could be extended to cover these.

Phylogeny

Taxonomic affinities have always been important criteria in selecting plants for host-specificity testing of potential agents, and the use of phylogeny was formalized by Wapshere (1974), who proposed the centrifugal phylogenetic testing strategy. This goes part of the way, but considers neither the phylogeny of the agent itself nor the dynamic interaction between the evolution of agent and host plant. Recent studies confirm that there is a strong correlation between agent and host-plant phylogenies (see Mitter *et al.*, 1991; Futuyma *et al.*, 1995; Briese, 1996; Kopf *et al.*, 1998) and that host range is a phylogenetically conservative trait in specialist phytophages (i.e. there are historical constraints to possible shifts in host range). An analysis of North American data by Pemberton (1999) has shown that all known non-target use of native plants by introduced biological control agents occurred on plants very closely related to the target weed (32/36 being congeneric). Furthermore, with the rapid expansion of molecular genetics, there are many new molecular phylogenies of plant groups, which give much clearer views of potential host relationships.

Host-screening procedures

Host-screening procedures for weed biological control have historically been extremely rigid, and have a very high degree of accuracy. Only one recent case is known where a released agent has subsequently attacked a plant in the field that had been originally cleared by quarantine host-specificity testing (Fowler *et al.*, 2000). Releases are sometimes made where tests indicate that non-target impact may occur, if the risk is considered minimal. A study by Willis *et al.* (1999) looked at field impact on non-target plants by some released agents and showed that previous glasshouse-based predictions of likely feeding of agents on non-target plants in Australia were accurate. Nonetheless, procedures are continuously being reviewed and improved (see Withers *et al.*, 1999), with increasing emphasis on understanding agent host-choice behaviour (see Marohasy, 1998) and the consequences of this on test design and protocol.

Risk scenarios

Several authors have attempted to assign categories or levels of risk from biological control agent introductions to non-target organisms (see Hopper, 1995; Cullen, 1997; Fowler *et al.*, 2000). In Table 9.4, we attempt to synthesize their ideas to produce a hierarchical set of risk categories for weed biological control. Fowler *et al.* (2000) found that only 2.4% of released agents would fall into the second risk scenario, in which the agent has some direct impact on a non-target species, of which 0.4% (2 cases out

Table 9.4. Hierarchy of increasing risk categories for agents released for the biological control of weeds. Each new risk category may include prior risk factors, e.g. the potential for flow-on effects through parasitoid/predator complexes can occur at 2.3 and 2.4, while competition with indigenous organisms is also a risk factor in 2.4.

1. Agent is completely monophagous: no direct non-target effect
    1.1. No indirect effects
    1.2. Possible indirect effects
        1.2.1. Target host is a significant resource for a third-party species, e.g. food, shelter, nest-site
        1.2.2. Agent may serve as a resource for native parasitoids/predators, leading to flow-on effects to other hosts within the complex
        1.2.3. Decline of target allows invasion by other weeds
2. Agent host range includes non-target species
    2.1. No overlap with non-target in introduced range due to temporal or spatial separation
    2.2. Agent overlaps with non-target plant, but feeding is transient or incidental
    2.3. Agent overlaps with non-target plants and can form persistent populations on them, but does not cause population consequences to host plant
        2.3.1. Competition with indigenous organisms exploiting non-targets as food resource
    2.4. Agent overlaps with non-target plants, can form persistent populations on them, and causes population consequences to host plant
        2.4.1. Direct reduction in density of non-target plant

of 492) are in category 2.4, in which the impact has potentially damaging population consequences for the non-target species. Other examples exist (e.g. Pemberton, 1999), so we suspect that it is more realistic to expect 3–4% of releases to fall into scenario number 2. Details and examples of risk categories are given below.

1. Agent is completely monophagous: no direct non-target effect

1.1. NO INDIRECT EFFECTS Most weed biological control agents fall into this category. Releases of such agents can proceed safely with evaluation only of the impact on target species.

1.2. POSSIBLE INDIRECT EFFECTS

1.2.1. Target host is a significant resource for a third-party species, e.g. food, shelter, nest-site. These are essentially 'conflict-of-interest' cases, and the critical decision is whether the weed should be controlled in the first place, given that it has some benefit. It does, however, have a place in an overarching risk analysis. Some suitable mechanisms for dealing with conflict of interest are in place for weeds, e.g. the Biological Control Act in Australia (see Paton, 1995). Where weeds have some economic benefit as well as a cost, e.g. the use of *Echium* and *Rubus* spp. for honey production, information on the cost of the weed problem relative to benefits derived from its use will be necessary. Biological control of both *Echium* and *Rubus* was allowed to proceed in Australia following formal cost–benefit analyses (Field and Bruzzese, 1985; Delfosse, 1989). In some cases the conflict may not be an economic one. For example, in the United States, the use of tamarisk for nesting by the endangered south-western willow fly-catcher held up biological control for a considerable time (Stenquist, 1999). However, successful control should see the original nest tree reappearing in the area, and the agent has now been approved for experimental release with close monitoring of potential impact on the bird. Similarly, biological control of *Emex* in Western Australia was posed as a potential risk to black cockatoos, which have adapted to feed largely on the seed of this exotic species (Scott *et al.*, 1999). Further information revealed that the cockatoos had extended their original range into the wheat belt where the weed occurred, where they still use only 2% of *Emex* production. Given that biological control should not affect the birds, it was allowed to proceed.

1.2.2. Agent may serve as a resource for native parasitoids/predators, leading to flow-on effects to other hosts within the complex. This was suggested as a possibility by Fowler *et al.* (2000), but they acknowledge that it is virtually impossible to assess and there are no known examples involving introduced agents. However, the use of ant-tended Homoptera in biological control of weeds has been questioned by Thum *et al.* (1997), as attraction of ants by these species can lead to predation on other control agents. This was a major factor in the decision not to release the fulgoroid plant-hopper, *Tettigometra sulphurea*, for control of *Onopordum* thistles in Australia (D.T. Briese, unpublished results).

1.2.3. Decline of target allows invasion by other weeds. Some other undesirable plant species have filled the gap created by reduction in density of the target weed, e.g. rangelands in parts of Idaho have become infested with *Centaurea* spp. following successful biological control of St John's wort (Campbell and McCaffrey, 1991). However, Syrett *et al.* (2000) point out that this should be seen more as a problem of overall land management than of biological control *per se*.

2. Agent host range includes non-target species

2.1. NO OVERLAP WITH NON-TARGET IN INTRODUCED RANGE DUE TO TEMPORAL OR SPATIAL SEPARATION Some non-target plants found to be potential hosts of a biological control agent may not co-occur with the target weed. This may be due to true differences in biogeographical range (i.e. different habitat, climatic requirements), or to the fact that the target weed has not yet reached its full range, in which case some risk may exist. This latter possibility can be clarified prior to release using climate-modelling techniques to predict the potential range of the target weed (see Maywald and Sutherst, 1997). Once it is clear that the target and non-target species are ecologically separated, releases can proceed safely with evaluation only of impact on target species. The indigenous Australian plant, *Heliotropium crispatum*, was infected by a rust fungus targeted against the introduced weed, *Heliotropium europaeum*, but, because of their different ranges and habitat requirements, the rust was approved and released safely (Hasan *et al.*, 1992).

2.2. AGENT OVERLAPS WITH NON-TARGET PLANT, BUT FEEDING IS TRANSIENT OR INCIDENTAL In some cases, feeding may occur on a non-target plant by only one particular stage of the agent and the plant cannot support its full life cycle. This may happen at the time of initial massive population explosions of the agent following release, such as occurred when *Cactoblastis cactorum* and *Chelnidea tabulata* attacked fruit crops near the heavily damaged target *Opuntia* populations (Dodd, 1940), and *Lantana* bugs similarly fed on sesame in East Africa (Greathead, 1968). These tend to be one-off or limited events and do not pose a long-term threat to the non-target plant. However, in some cases, such as *Zygogramma bicolorata* adults feeding on neighbouring sunflower in India after huge outbreaks of beetles had defoliated target *Parthenium* populations, the incidental costs to individual farmers can be very high (McFadyen and Heard, 1997).

2.3. AGENT OVERLAPS WITH NON-TARGET PLANTS AND CAN FORM PERSISTENT POPULATIONS ON THEM, BUT DOES NOT CAUSE POPULATION CONSEQUENCES TO HOST PLANT This appears to be the most common risk scenario and, generally, the non-target is a less-preferred host. There are several interesting examples. Field studies by Berentson (1999) confirmed the pre-release assessment that feeding by the mite, *Aculus hyperici*, on non-target native *Hypericum gramineum* in Australia was not threatening field populations of the latter. Mites persist in low numbers on *H. gramineum*, which in fact could act as a sink, providing sources of material to colonize nearby weedy outbreaks of *Hypericum perforatum*, upon which they do build up and cause damage. The overall effect may therefore be beneficial. Moths of *Euclasta whalleyi*, released for the control of rubbervine in Australia, will also oviposit and the larvae will feed on related native vines, but only in the vicinity of large rubbervine populations (McFadyen and Heard, 1997). The weevil, *Rhinocyllus conicus*, can breed on several native US *Cirsium* species in addition to its target weed (Turner *et al.*, 1987), but Herr (1999) has shown that, where there is asynchrony between the life cycles of agent and host, there should be no population effect on the plant (see Gassmann and Louda, Chapter 8, this volume). However, the fact that the agent can persist on the non-target may provide a platform for selection of better-adapted individuals and evolution of the agent population on the non-target, such as reported by Andres (1985) for *Chrysolina quadrigemina* on the ornamental *Hypericum calycinum* in California, USA. This would need isolation from the primary weed host to occur, but could lead to upgrading of risk category in the longer term. There could also be competition with indigenous organisms exploiting non-targets as a food resource (see Section 2.4.2 below).

2.3.1. Competition with indigenous organisms exploiting non-targets as a food resource. Louda *et al.* (1997) observed that increases in the density of the introduced capitulum weevil, *R. conicus*, following its colonization of a non-target native *Cirsium* species in the United States, led to reduced density of a native tephritid fly that also developed in *Cirsium* capitula. This type of interaction is an indirect effect of the agent, brought about by competition for a shared resource (see Gassmann and Louda, Chapter 8, this volume).

2.4. AGENT OVERLAPS WITH NON-TARGET PLANTS, CAN FORM PERSISTENT POPULATIONS ON THEM, AND PROMPTS POPULATION CONSEQUENCES TO THE HOST PLANT In these cases, the non-target and target plants are generally both highly preferred hosts. Under such circumstances, the population of the agent is no longer determined principally by the target species, but rather by a complex, of which the target is only one member. High numbers may well be maintained on one or more species to the detriment of any individual species, particularly if it is a preferred host. Where this is the target, control may be extremely effective. Where it is not, a native non-target species may suffer considerable impact (Cullen, 1997).

2.4.1. Direct reduction in density of non-target plant. Direct reductions in plant density of non-target species have been occasionally reported. *C.*

cactorum has been held responsible for greatly reducing populations of a rare endemic cactus species in Florida (Bennett and Habeck, 1995). Louda and Arnett (1999) have demonstrated population effects on one species of *Cirsium*, in which there is synchrony between flowering phenology and *R. conicus* activity. In both cases, the result would have been foreseeable from host-specificity testing, and realization of the risk has been a matter of judgement, rather than problems with the testing procedure (see Gassmann and Louda, Chapter 8, this volume). For example, *Neurostrota gunniella* has been released for the biological control of *Mimosa pigra* in Australia, despite the fact that it is known to attack related native *Neptunia* species. The argument was that undesirable direct population consequences on these native species would be outweighed by the desirable indirect effect from control of *Mimosa*, which was threatening the habitat of the natives. However, the agent was not released in Thailand, where *Neptunia oleracea* is an important vegetable and attack by *Neurostrota* could have had serious economic consequences (Forno *et al.*, 1999).

Risk management

In the field of risk analysis, risk management is what is done to minimize harm when a hazard is realized, and is commonly practised where hazardous events are difficult to predict. Risk management reduces risk by: (i) reducing the potential impact of the hazard (e.g. earthquake proofing a building); (ii) reducing the probability of the hazard occurring (e.g. installation of dual controls in a driving-school car); or (iii) reducing exposure (e.g. through the use of containment facilities in laboratories where radioactive materials are handled).

Clearly, there are parallels in weed biological control. For direct non-target effects of biological control of weeds, it is hard to imagine a form of remedial action. If there is damage to a crop plant that might be regularly sprayed for other pests, it could be argued that this might eliminate the present risk. However, we are then locking the farmers into a pesticide cycle and taking away their chance to make technological advances that would specifically target the primary pest, as our agent would still be there damaging the crop. If there is damage to a native, it may be possible to carry out a species rescue plan to establish new populations. However, it would be better simply to ensure that there will be no situation giving cause for remedial action prior to the decision to release. In other words, we should preferably introduce only highly specific agents. On the other hand, undesirable indirect effects are a possibility even in the best-managed projects. They may be mitigated by management plans; for example in the tamarisk controversy, a vegetation management plan to actively restore native vegetation and favour nesting by the willow fly-catcher would have been an application of the risk management approach (method no. (i), above).

Risk communication

Background

Despite considerable publicity on the negative effects of weed biological control in recent years, it is still possible to hear a prominent environmentalist refer to biological control of weeds as the last best hope (Randall, 1999). Yet this same presenter made clear the need for good dialogue between proponents and environmental agencies. The old model for risk communication involved experts speaking from on high to a credulous and accepting audience. However, experts are now more likely to be listened to very critically, or even distrusted. Instead, active dialogue with regulators, stakeholders and the public is more fruitful. For biological control, much risk communication centres on an interaction with regulatory authorities to arrive at a decision on whether to release an agent.

Release application procedures in different countries

All the countries with a strong tradition of weed biological control have processes that allow for two-way dialogue with regulatory authorities. The way in which the authority is set up and the way in which the dialogue can take place varies and in many cases is still evolving (e.g. the USA and New Zealand are developing more complex application procedures, while South Africa has had a recent move to consultation rather than in-house decisions). In general, in North America the risk assessment is reviewed by designated experts and by a Technical Advisory Group prior to a decision being made. The Australian model is arguably more interactive than that, as the regulatory agency acts as a facilitator; cases are reviewed by 21 expert organizations, including conservation agencies and, where disagreement with the proposal occurs, the individual reviewing organizations enter negotiations with the proposing organization and attempt to resolve the problem (see Paton, 1995). Thus, a decision is generally not given without this level of consultation and frequently new information or extra work enables the proposal to be accepted.

Another difference is that the Australian model deals only with safety (i.e. it is based on host range), not effectiveness. The trend, however, is towards greater transparency and more rigid scrutiny with new regulatory frameworks being developed in New Zealand and the USA (Anonymous, 1997; Knutson and Coulson, 1997). In New Zealand under the Environmental Risk Management Authority (ERMA; see Anonymous, 1997), the proponent has to demonstrate monetary and non-monetary benefit, as well as developing an environmental impact statement for the short term and long term effects on the environment, including other organisms.

Moreover, this process involves wide public consultation; anyone can contribute, not just experts. The United States legislation seems to be approaching that of New Zealand, as draft environmental assessments are now required before permission is given to release biological control agents (Rizvi, 1999). The issue here is the level of consultation needed. Too broad and it risks bogging down the whole process; too little and it can be criticized as being unsafe or paternalistic.

Countries with shorter histories of using biological control (especially developing countries) do not have regulatory processes specifically for the introduction of biological control agents, but, as McFadyen (1998) states, they can make use of the recent FAO International Code for the Import and Release of Exotic Biological Control Agents (Labrada, 1996; Greathead, 1997). Innovations in biological control risk analysis by Australia, Canada, New Zealand, South Africa and the United States will probably flow on to these countries.

Precautionary principle

In 1992, governments (federal, states and local governments) in Australia agreed to follow the precautionary principle (PP) as part of a commitment to ecologically sustainable development. There are many formulations of the principle, but that adopted by these governments was:

> Where there are threats of serious or irreversible environmental damage, lack of full scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation. In the application of the precautionary principle, public and private decisions should be guided by: (1) careful evaluation to avoid, wherever practicable, serious or irreversible damage to the environment; and (2) an assessment of risk-weighted consequences of various options.

Other governments around the world have adopted the PP to a greater or lesser degree, and it was recently incorporated into the international Biosafety Protocol. It is certainly a watchword for environmental groups who are potentially stern critics of biological control. However, there is no agreement on the precise formulation, and there are varied opinions on whether the PP is mainly scientific, mainly legal or a combination of both. There will have to be many debates over the next few years if we are to arrive at a widely acceptable formulation. From a biological control point of view, we could probably argue that in carrying out several years' work to assess specificity of an agent, evaluate this information and weigh up risks, we are applying the PP, at least according to the version quoted above. It would seem to be an advantage for risk communication of biological control if the discipline were to engage actively in discussions on defining the PP, with a view to subscribing to it formally.

Good and bad risk communication

Failures in risk communication can be costly. The financial cost of the BSE (bovine spongiform encephalopathy) crisis in the UK is estimated at around US$5 billion, a cost that could have been reduced with more effective risk management and communication procedures (Powell, 1999). Good risk communication is probably just as important as risk assessment and risk management, and it is down to scientists to take primary responsibility for it if their work is to be accepted by society. The message from the worlds of food safety and the chemical industry is that we must: (i) establish credible, open and responsive regulatory systems; (ii) communicate effectively about the nature of risk; (iii) make demonstrable efforts to reduce levels of uncertainty and risk; and (iv) never make statements implying that very low probabilities mean no risk at all. We should be aware that there is always more to a risk issue than just the science. ‘Educating the public’ about the mysteries of scientific research is no substitute for sound risk communication practice (Powell, 1999). Given that risk perception changes with culture, gender and degree of education, it may be useful for our discipline to research how the risks of our actions are perceived by different sections of society, the better to formulate our risk communication practices. There is another use of the term risk communication that means communicating the level of risk to stakeholders to assist in risk management; e.g. communication of the risk associated with tamarisk control may encourage the provision of nesting sites for willow fly-catchers.

Monitoring

Monitoring for non-target or undesirable indirect effects of our biological control agents is a worthy aim that is likely to founder in practice on the limited resources of the average biological control project, and the technical difficulty of measuring interactions between two or more trophic levels (e.g. Lonsdale and Farrell, 1998). The rarity of published quantitative data on the impacts of our agents on the target weed is not the result of laziness or ineptitude, but of the real difficulties in resourcing and executing studies that can tease out the effects of an agent against the natural spatial and temporal fluctuations in weed populations. Measurement of impact on target plants is hierarchical: (i) establishment of agent; (ii) damage caused by agent; and (iii) population impact of agent on target (see Syrett *et al.*, 2000). Measurement of impact on non-targets would use the same sequence. The problem is that we rarely get beyond the second step: establishing that damage is caused to individual plants. It is not sufficient to demonstrate an impact, say, on seed output, for plant populations are rarely limited by seed. Space does not allow us to consider here methodologies for measuring the impact of biological control on plant populations (see Lonsdale and Farrell, 1998; Syrett *et al.*, 2000; and references therein), but it is worth examining here the resources that would be required to monitor the effect of an agent on the conservation status of a rare plant. The IUCN Red List categories – vulnerable (VU), endangered (EN) and critically endangered (CR) – are precisely enumerated in terms of population change, extent or size (Walter and Gillett, 1998). We might study a native plant population using 1-m^2 quadrats. Let us assume that natural variability, measured by the coefficient of variation, might be in the order of 80% at this scale. Imagine measuring the populations before and after the arrival of the insects, using some permanent quadrats. We could probably use a paired *t*-test to test the significance of a decline in density. How many quadrats would we have to monitor to detect a change from non-Red Book to the various levels of endangerment? A species is 'VU' if it shows a decline in population size of 20%, 'EN' if it falls by 50% and 'CR' if it falls by 80%. Using an algorithm for determining sample size suggests that we would need 128 quadrats to monitor a decline from normal to 'VU', 23 from normal to 'EN', and 10 from normal to 'CR'. While measuring declines to 'EN' and 'CR' seem within reach, that to 'VU', which would in itself be a grave consequence of biological control, would be very taxing, particularly as the trend may have to be measured over 10 years (Walter and Gillett, 1998). It would be best to avoid the need for such studies altogether by introducing only highly specific agents.

Synthesis

What then does the field of risk analysis have to tell us in weed biological control? Comparative risk analysis tells us that the hazard of biological control agents as pests is of little significance next to the number of other exotic pests. However, risk communication tells us that, because there is increasing distrust of scientists, and increasing concern about the environment, any environmental hazard resulting from our actions as experts is likely to receive a disproportionate level of opprobrium. The tendency for scientists, in response to this criticism, will be to emphasize risk assessment and monitoring, because these are the most 'scientific' disciplines of the five. However, as is shown above, ecological risk assessment and monitoring are likely to be tortuous, expensive and involved, particularly for indirect effects. Nor will more biological control science solve the problem of a lack of trust. Instead, we should focus on good risk communication and risk management practice and: (i) decide on weed targets that will have wide ownership, by consulting particularly with environmentalists, who would tend to be our sternest critics. This would mean that there would be general agreement that the indirect effects of biological control would on balance be very desirable, in this particular case; (ii) understand the concerns of our critics and our supporters, and how their perceptions vary by group, to improve our ability to engage in a dialogue with them; (iii) introduce only highly specific agents so that the most likely hazards are undesirable indirect effects, which can be easily counterbalanced with desirable ones because of the wide ownership of the weed as a problem; (iv) use a risk management approach to maximize the benefit/risk ratio, especially for indirect effects; and (v) support a policy framework governing biological control releases that involves wide consultation with environmental agencies, and veto powers over release. The proponents should have only an advisory role.

All this would result in very low risk of undesirable direct effects (i.e. non-target attacks), and a high probability that any undesirable indirect effects would be vastly outweighed by desirable ones. One consequence would be that certain weeds would become obviously unsuitable for biological control. However, this would be clear from the outset, as consultation would fail to gain approval for that weed as a target. This would certainly be preferable to spending resources on biological control agents, only to discover at the end that they would never be released.

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10

Incorporating Biological Control into Ecologically Based Weed Management

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Abstract

Ecologically based weed management involves the identification and manipulation of processes that direct community dynamics. Of the many processes occurring in an ecosystem, those with the highest likelihood of causing change in a desired direction should be modified to allow predictable outcomes. Biological control agents modify interference, stress and dispersal. Incorporating biological control into ecologically based weed management is critical when and where at least one of these three processes drives plant community dynamics. If other processes dominate succession, it is unlikely that biological control will assist in establishing or maintaining desired plant communities. Two models, one conceptual and one mathematical, are proposed for understanding any process modifying factors influencing the plant community. These ecologically based models can be used to direct the development of integrated weed management with predictable outcomes. Assessment of biological control, or any management strategy, must be based on the predicted impacts on the organization, structure and function of the ecosystem.

Introduction

Integrated weed management (IWM) became an accepted and frequently used term by weed scientists in the 1970s. Walker and Buchanan (1982) defined integrated weed management as ‘the application of many kinds of

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technologies in a mutually supportive manner'. It involves the deliberate selection, integration and implementation of effective weed control measures with due consideration of economic, ecological and sociological consequences. It is a multidisciplinary, ecological approach to managing weed infestations. The founding principles of IWM are that natural weed controlling processes can be manipulated to increase their effectiveness, and chemical controls should be used only when and where natural processes of control fail to keep weeds below economic injury levels (Rabb and Guthrie, 1972). IWM in its original sense of ecologically based management has not been developed or implemented on a wide scale (Kogan, 1986; Cate and Hinkle, 1993). The objective of this chapter is to discuss methods for incorporating biological control into ecologically based weed management.

Management objectives

Historically, pest management has evolved for cropping systems and has focused on controlling pests. Today, many land managers focus weed management simply on controlling weeds, with limited regard for the existing or resulting plant community. On grass and forest lands, the effectiveness of various weed management strategies depends on how land is used. Weeds must be considered in establishing land-use plans. This implies that strictly killing weeds is an inadequate objective, especially for large-scale infestations. A generalized objective for ecologically based weed management is to develop and maintain a healthy plant community that is relatively weed-resistant while meeting other land-use objectives, such as forage production, wildlife habitat development or recreational land maintenance (Sheley *et al.*, 1996). A healthy, weed-resistant plant community consists of a diverse group of species which occupy most of the niches (Tilman, 1986). Diverse communities capture a large proportion of the resources in the system, which pre-empts their use by weeds (Pyke and Archer, 1991; Sheley and Larson, 1996). Plant communities with representatives from various functional groups also optimize ecosystem functions and processes regulating plant community stability. Ecologically based weed management programmes must focus on establishing and maintaining desired functional plant communities. Thus, development and adoption of management strategies promoting desirable species offers the highest likelihood of sustainable weed management.

Need for predictive capability

The success of any weed management programme will depend on how closely the post-management species and/or functional group composition matches that stated in the objectives. Ecologically based weed management requires the ability to predict community responses to natural and imposed conditions (Kedzie-Webb, 1999). Predictive capabilities allow ecological and economic assessment of various strategies. Without predictive capabilities, the decision to impose a particular strategy is either based on prior experience or is arbitrary. Furthermore, risk assessment of any practice, including biological control, must be based on models that provide an understanding of the plant community after implementation. An understanding of the organization, structure and function of the post-management plant community is central to assessing the indirect effects of any weed management strategy because it determines the sustainability of the ecosystem. Predictive capability will require a mechanistic understanding of the ecological principles directing plant community dynamics.

Mechanisms and processes directing plant community dynamics

It has long been recognized that plant community composition changes over time (Clements, 1916). Earlier studies focused on describing those changes and relating them to plant strategies and traits in order to develop the ability to predict succession (MacArthur, 1962; Grime, 1979). More recently, ecologists have recognized that the ability to predict succession requires an understanding of the mechanisms and processes directing plant community change (Allen, 1988; Louda *et al.*, 1990; Luken, 1990). Connell and Slatyer (1977) proposed three mechanisms of succession: facilitation, tolerance and inhibition. These mechanisms comprise a wide variety of processes, which influence succession.

Pickett *et al.* (1987) developed a hierarchical model of succession, which includes the general causes, controlling processes and their modifying factors (Table 10.1). They proposed three general causes of succession: disturbance, colonization and species performance. The process of disturbance plays a central role in initiating and altering successional pathways, although a unified disturbance theory has not been developed (Pickett and White, 1985). Natural disturbances, such as landslides, fire and severe climatic conditions, initiate, retard or accelerate succession. For example, Tyser and Key (1988) found that spotted knapweed (*Centaurea maculosa* Lam.) was capable of expanding into Glacier National Park, USA, by first establishing in small patch disturbances created by wildlife. Once established, large-scale disturbance may have allowed large-scale invasion. The size, severity, time intervals and patchiness of disturbance, in part, determine the successional trajectory of plant communities.

Colonization, the availability and establishment of various species, is another important cause of succession. Processes directing colonization are dispersal, propagules and species-specific establishment characteristics.

Table 10.1. Causes of succession, contributing processes and modifying factors (modified from Pickett *et al.*, 1987).

Causes of succession	Processes	Modifying factors
Site availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species availability	Dispersal	Dispersal mechanisms and landscape features
	Propagules	Land use, disturbance interval, species life history
Species performance	Resources	Soil, topography, climate, site history, microbes, litter retention
	Ecophysiology	Germination requirements, assimilation rates, growth rates, genetic differentiation
	Life history	Allocation, reproduction timing and degree
	Stress	Climate, site history, prior occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

Factors modifying colonization include dispersal mechanisms, landscape features, species life histories and vegetative reproductive plant parts. The combination of the modifying factors interact to help determine the outcomes of succession. Species performance, the relative growth and reproduction of species, plays a critical role in determining plant community dynamics. Processes associated with the relative performance of species within the plant community include availability, ecophysiological processes, life history, stress and interference. Factors that modify these processes are site, climate, microbes, litter retention, germination requirements, growth rates, genetic differentiation, reproductive allocation, herbivory, competition, allelopathy and natural enemies.

Ecologically based weed management attempts to understand the conditions, mechanisms and processes, and their modifying factors, well enough to allow for predictable transitions. In any system, there may be many processes and interactions affecting plant community composition. However, weed scientists and managers must identify those mechanisms and processes that dictate the direction of succession. The objective is to understand and manipulate the factors that modify processes to favour desired species. Ultimately, the goal is to direct plant communities on a trajectory towards more desirable plant communities (Rosenberg and Freedman, 1984; Luken, 1990). This is the ecological basis for IWM.

Incorporating biological control into ecologically based weed management

The extent to which biological controls should be incorporated into weed management programmes depends upon their ability to modify processes directing succession in a particular system. Natural enemies have the capability to modify interference (Jacobs *et al.*, 1996; except see Calloway *et al.*, 1999), stress (Rees *et al.*, 1996) and dispersal (Story *et al.*, 1989). Studies should focus on understanding the key processes directing succession and the role that potential biological control agents play in altering the important processes. In situations where the key controlling processes are those that can be modified by natural enemies, incorporating biological controls are appropriate. For example, in many areas of the United States, St John's wort (*Hypericum perforatum* L.) has been effectively controlled by two species of beetles (*Chrysolina quadrigenina* (Suffr.) and *Chrysolina hyperici* (Foster)). Conversely, incorporating biological controls into ecologically based weed management in situations where agents do not affect key processes is inappropriate. This may be the case for spotted knapweed, where competition for resources determines its dominance (Herron *et al.*, 2000). Currently available biological control does not significantly affect competitive relationships in spotted knapweed-infested communities.

Modelling and predicting weed management's influence on community dynamics

Successional weed management

Managing succession requires knowledge of three components corresponding to the three general causes of succession: disturbance, colonization and species performance (Rosenberg and Freedman, 1984; Pickett *et al.*, 1987; Luken, 1990; see Table 10.1). Within the limits of our knowledge about the conditions, mechanisms and processes controlling plant community dynamics, these three components can be modified to allow predictable successional transitions. We can design the disturbance regime and attempt to control colonization and species performance through management. Successional management must be viewed as an ongoing process moving from one successional component to the next or repeating a single component through time (Fig. 10.1). This model is driven by both naturally occurring and human-induced processes and thus is robust enough to allow incorporation of virtually any management decision.

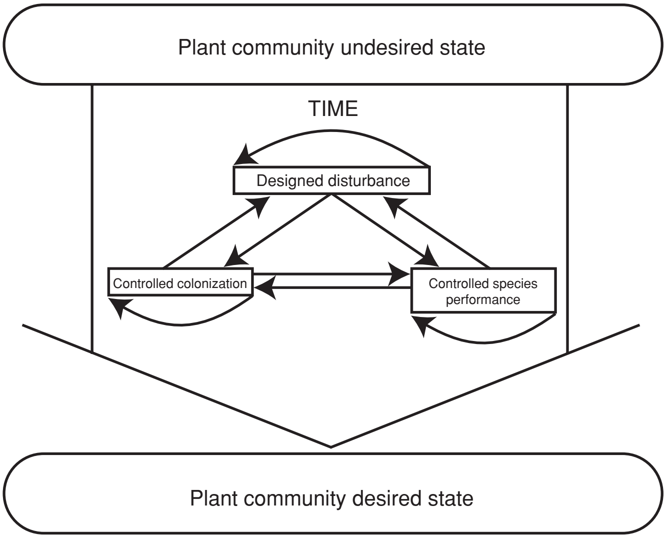

Fig. 10.1. Components of a successional weed management model. Straight lines indicate sequential steps; curved lines indicate repeated stops (modified from Rosenberg and Freedman, 1984).

Designed disturbance

Theories are emerging that suggest large-scale disturbance and patch dynamics contribute to the invasion of intact (pristine) plant communities by rangeland weeds. For example, Tyser and Key (1988) found that spotted knapweed was capable of expanding into grassland communities in Glacier National Park in Montana, USA. Small patch disturbances created by wildlife and roadside activity allowed individual spotted knapweed plants to establish. We believe that the aggressive characteristics of many rangeland weeds allow maintenance of small populations. Subsequent large-scale disturbances, such as fire or drought, create safe sites and reduce the competitive ability of the perennial species, which favours large-scale invasion by weeds. Succession may be permanently altered (Svejcar and Tausch, 1991). In the case of spotted knapweed, large-scale disturbance may not be necessary for invasions. Patch disturbances, such as roadsides, may be sufficient to initiate invasions.

Designed disturbances include activities that are initiated to create or eliminate site availability and are aimed at initiating and controlling succession. Weed management strategies have included designed disturbance, such as cultivation, burning and herbicide applications, for decades. However, in successional management, designed disturbance is used to alter successional trajectories and to minimize the need for continuous high energy inputs. The utility of any specific designed disturbance in successional weed management will depend on the site, plant community type, invading weed species, site history, season, climate (macro and micro) and the management goals.

In the case of spotted knapweed invasion into Glacier National Park, successional planning will require identification of disturbance thresholds and modification of the disturbance. In this example, if roadside disturbance provides a staging area for weed invasion, emphasis could be placed on roadside revegetation with competitive native perennial species. Establishment of a competitive native community should reduce site availability for the weed species.

Controlled colonization

Controlled colonization is the intentional alteration of availability and establishment of various plant species. Colonization may be influenced in a positive or negative manner depending on the species and successional goals. Controlled colonization efforts are directed towards influencing seed banks, propagule pools, and regulation of safe sites for germination and establishment of desirable species. Weed seed banks can be depleted through attrition if seed production is prevented or significantly reduced. Olson *et al.* (1997) found that the number of spotted knapweed seeds in the soil was reduced after 3 years of intensive sheep grazing, resulting in decreased weed density.

In another example, two seed-feeding flies (*Urophora affinis* Frfld. and *Urophora quadrifasciata* (Meig.)) have been shown to reduce spotted knapweed seed output by up to 80% (Harris, 1980). Weed seed dispersal can also be limited by not driving vehicles through weed-infested areas when seeds are present, not grazing livestock in weed-infested areas during flowering and seeding or holding animals for 14 days before moving to uninfested areas, and using hay free of weed seeds (Sheley *et al.*, 1995).

It is possible that introducing seeds of desirable species in small amounts each autumn or winter to mimic natural seeding may allow colonization by increasing the probability that seeds are available during favourable environmental conditions. Because weed seeds can be dispersed by livestock (Wallander *et al.*, 1995) and hay (Zamora and Olivarez, 1994), using livestock to introduce seeds of desirable species in favourable patches may be feasible, and offers a low-input method for controlling colonization. Conceivably, managers could add seeds of desirable species into hay during fall and winter feeding periods to be spread throughout a pasture. In addition, hoof action by livestock may create safe sites, enhancing seedling establishment.

Controlled colonization may include introduction of certain less desirable, but ephemeral, species to facilitate establishment of desirable species by creating safe sites for germination and seedling survival. Introduction of early successional species may cause changes in soil properties that would facilitate later successional or more desirable species (Allen and Allen, 1988). A specific example of controlled colonization to direct succession is presented by De Pietri (1992). The alien species mosqueta rose (*Rosa rubiginosa* L.) can speed the recovery of degraded native forests in Argentina by serving as a nurse plant for native species. The decision not to control mosqueta rose or to place propagules on a site would constitute a controlled colonization decision drawing on the facilitation principle as a mechanism driving succession (Connell and Slatyer, 1977).

Controlled species performance

Controlled species performance involves manipulating the relative growth and reproduction of plant species in an attempt to shift community dynamics in a desirable direction. Biological and chemical weed control, grazing, plant and plant-part removal, altering resource availability and competitive plantings are techniques for creating differential species performance.

Huffaker (1967) provides a classic example of biological control. In many areas of the United States, St John's wort has been effectively controlled by two species of beetles. Many herbicides selectively control weeds (Fay *et al.*, 1995). In both cases, plant communities can be shifted towards desirable species provided that propagules are present and establishment occurs. Most animals have preferences for certain forages. Selective grazing by herbivores can shift the competitive balance of plant communities (Crawley, 1983; Louda *et al.*, 1990). For example, in some situations, leafy spurge (*Euphorbia esula* L.) can be controlled by sheep or goat grazing (Johnston and Peake, 1960). Appropriate grazing by animals preferring weeds can shift the plant community towards more desired grasses (Lacey *et al.*, 1984). On the other hand, cattle grazing can selectively reduce grass competitiveness, shifting the community in favour of weeds (Sheley *et al.*, 1997).

Resource availability to plants may be used to influence succession. In some cases, changes in plant communities are related to resource availability and the relative ability of species in the community to extract those resources. To quote Tilman (1988), 'Because each plant species is constrained to being a superior competitor for particular resource levels, the forces that determine resource levels are critically important in determining vegetation patterns'. Thus, another potential successional management strategy would be to influence species performance via soil nutrient manipulation. McLendon and Redente (1991) demonstrated that additions of nitrogen inhibited succession from annual to perennial species in a sagebrush steppe site in north-western Colorado, USA. They concluded that dominance by annuals during the early stages of secondary succession was related to high nutrient availability. One successional management strategy might be to reduce nutrient availability.

The potential of reducing nutrient availability to foster succession has not been adequately explored. Most of the emphasis in nutrient management has been on increasing availability. However, annual cropping systems have been used to reduce nitrate leaching from agricultural fields. It may be possible to use species with demonstrated abilities to sequester nitrogen, such as rye (*Secale cereale* L.) or mid-successional species to reduce resource availability. Species composition can directly influence nutrient dynamics. Tilman and Wedin (1991a) studied a range of species with different successional niches, and found that late successional species were very competitive for nitrogen. Late successional species have high below-ground biomass. This creates soils with high carbon/nitrogen ratios, and consequently low nitrogen mineralization. The early successional species were poor competitors for nitrogen, but persisted by maintaining rapid growth rates and high seed production. When grown in pair-wise competition experiments, the late successional species displaced early- to mid-successional species (Tilman and Wedin, 1991b). The ability of a species to lower soil quantities of extractable ammonium and nitrate accounted for the results of the competition trials. Oomes (1990) presented a specific example of successional management via reduced nutrient availability. He restored species-rich grasslands from fertilized agricultural grasslands that contained relatively few species. The applied treatment involved mowing twice a year and removing the harvested material. Depending on the site, 3–8 years were required to reduce biomass and nitrogen yield to the point where species richness could increase.

Examples

Several schematics using successional weed management are shown for leafy spurge-infested rangeland in Fig. 10.2 (Larson and McInnis, 1989; Sheley and Jacobs, 1997). In these examples, the plant community prior to weed management is composed of: (i) 85% leafy spurge and 15% Kentucky bluegrass (*Poa pratensis* L.); or (ii) 50% leafy spurge, 30% suppressed native species and 20% bluegrass. Two successional weed management systems are shown for each situation. In these examples, the resulting plant community is influenced by both the weed management system and the initial plant community. Weed management actions should be selectively integrated to ensure that the three components of the successional management model are addressed in a complementary manner, based on the composition of the existing plant community.

The successional weed management model presented in this chapter allows for integration of currently available tools. Unfortunately, with conceptual models of this type, there are seldom large comprehensive research projects that have tested all possible options for a particular plant

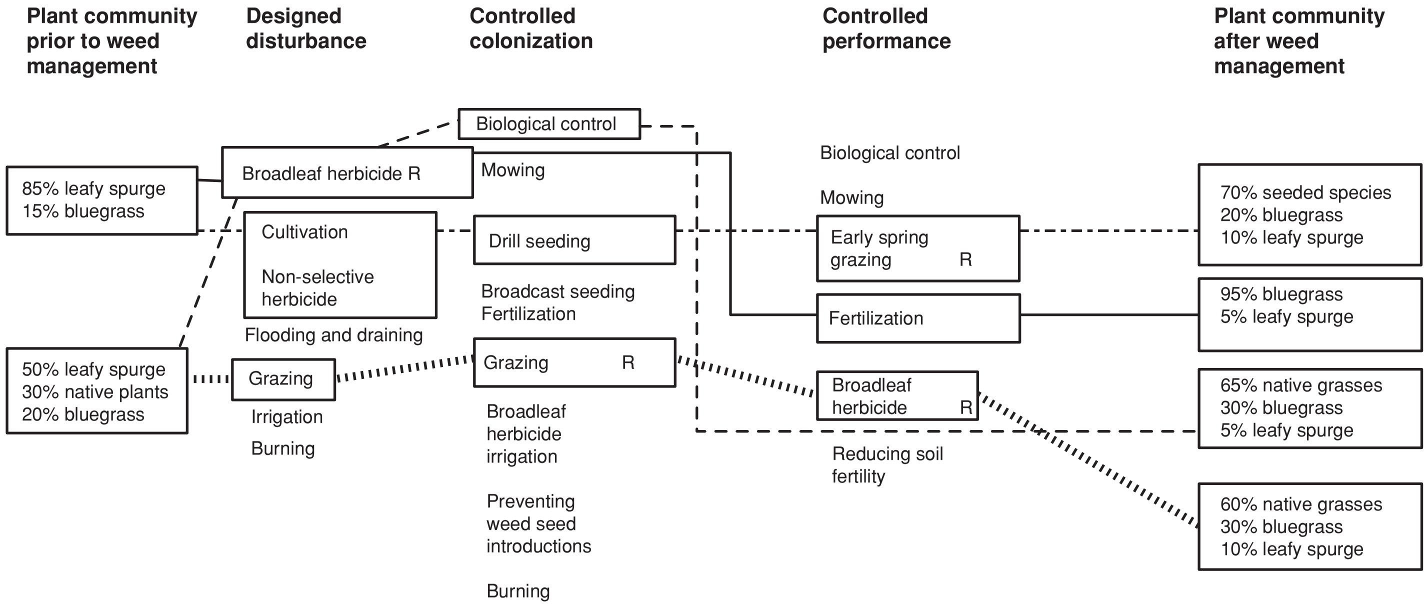

Fig. 10.2. Four spotted knapweed management scenarios' illustrating successional weed management and its use in weed management planning. Each arrow type corresponds to one management scenario. R indicates that the technique is repeated.

community. Development of successional weed management plans will require the use of existing research information, management experience and monitoring of successes and failures to adjust future plans.

Life-history models

Life-history tables have been used in order to predict the dynamics of weed populations based upon the influence a particular management strategy has on a process (Fig. 10.3). These tables consist of a series of states (growth stages) and a series of transitions that represent the flow of individuals from one growth stage to the next. Each state represents the number of individuals of a particular growth stage that are present per unit area. The transitions have values that correspond to the proportion of individuals that advance from one state to the next within a generation. In management, the proportion of individuals that advance from one stage to the next can be altered by modifying the important processes occurring at that transition. The state value is multiplied by the transition value to yield the number of individuals that advance to the next state. A single-species life-history table was used to demonstrate the response of leafy spurge populations to picloram (Bowes and Thomas, 1978). A second single-species life-history table was used to simulate development of leafy spurge populations from the introduction of propagules and the response of leafy spurge populations to the reduction of particular transition values (Watson, 1985). The transition values were constant in these earlier models. Density-dependent factors were not considered. A later model incorporated intraspecific density dependent transition functions (Maxwell *et al.*, 1988). Sensitivity analysis was run on this model to identify vulnerable areas in the life cycle of leafy spurge. More recently, Sheley and Larson (1994) developed a two-species life-history table that was used to compare the population dynamics of two winter annuals, cheatgrass (*Bromus tectorum*) and yellow starthistle (*Centaurea solstitialis*). This information was developed into a preliminary computerized tool to assess integrated weed management (Maxwell and Sheley, 1997).

A conceptual three-species life-history table has been developed that will serve as a generalized system for understanding multi-species relationships on rangeland (Fig. 10.4). The three species in the life-history table are Kentucky bluegrass, western wheatgrass (*Agropyron smithii*) and leafy spurge. These grasses are often found growing in association with leafy spurge and offer an excellent opportunity to study multi-species interactions (Nowierski and Harvey, 1988). The stages in the model include: number of seeds in the seed bank, number of seedlings, number of vegetative and crown shoots, number of flowering shoots and grass biomass. Life-history tables have been incorporated into computer programs that are capable of conducting the mathematical computations necessary

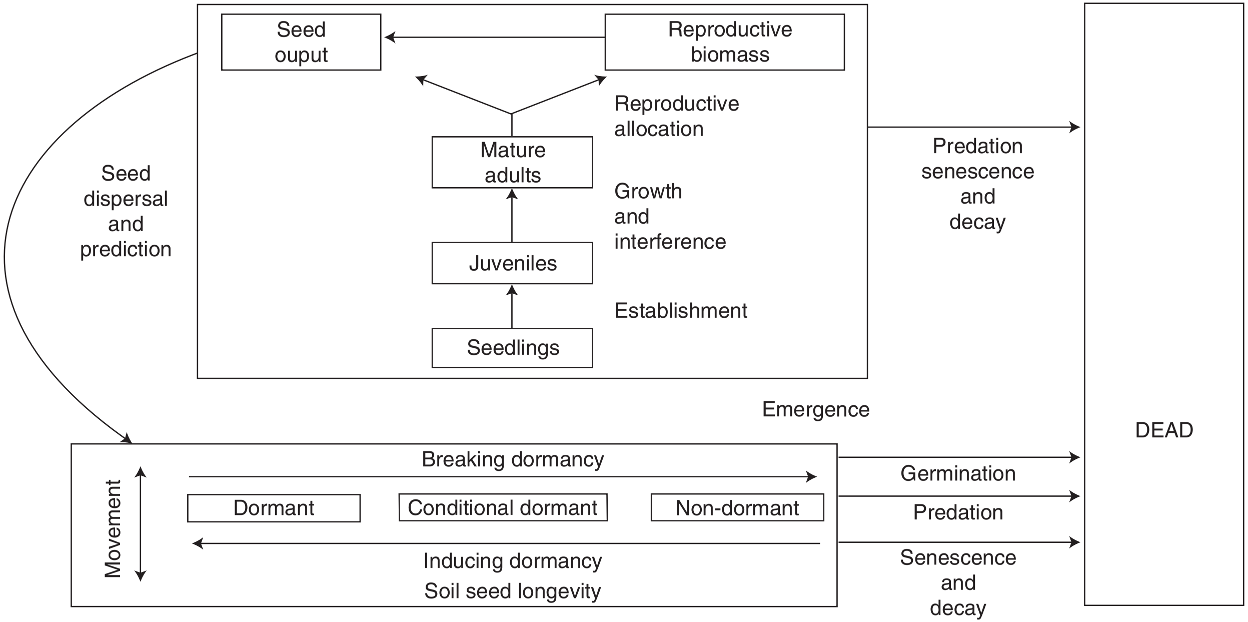

Fig. 10.3. A conceptual model of an annual plant life cycle. Boxes represent life-history stages; arrows represent processes that regulate species performance among the life-history stages (modified from Radosevich and Roush, 1990).

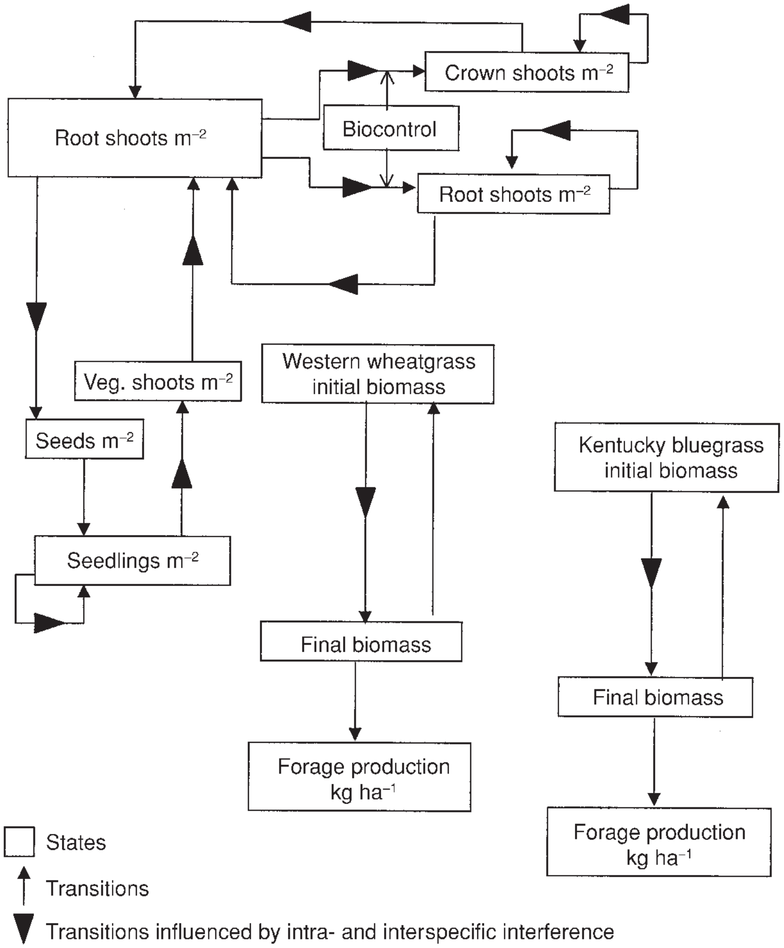

Fig. 10.4. Three-species model for leafy spurge, Kentucky bluegrass and western wheatgrass.

for tracking populations and plant communities through time (Watson, 1985; Maxwell and Sheley, 1997).

The values necessary for developing a model include numerous life-history parameters and species competitive relationships. For example, the number of leafy spurge seeds that a reproductive shoot produces is dependent on the abundance and competitive relationships of various components of the plant community. This prediction of the number of leafy spurge seeds per shoot can be mathematically described as (Firbank and Watkinson, 1985):

$$SPS = SPS\mathrm{max}\,[1 + \alpha\mathrm{max}(FS + \alpha_1 VS + \alpha_2 VB + \alpha_3 VW)]^b$$

where *SPS* is the mean number of seeds produced by an individual leafy spurge shoot, *SPS*max is the number of seeds that a leafy spurge shoot produces when it is not influenced by competition, αmax represents the maximum area of leafy spurge plants that are not influenced by competition, and *FS* and *VS* are the final number of leafy spurge flowering and vegetative shoots m^{-2}, respectively, in the current generation. *VB* and *VW* are the final volumes of Kentucky bluegrass and western wheatgrass, respectively, in the current generation. α_1, α_2 and α_3 are the competition coefficients for the effects of vegetative shoots of leafy spurge, Kentucky bluegrass volume and western wheatgrass volume on *SPS*, respectively; *b* describes the efficiency of resource use by the community.

The model contains a series of formulae that predict densities of leafy spurge shoot types as well as Kentucky bluegrass and western wheatgrass biomass over multiple generations (Fig. 10.5). Simulations can be run without and with the incorporation of procedures that modify processes.

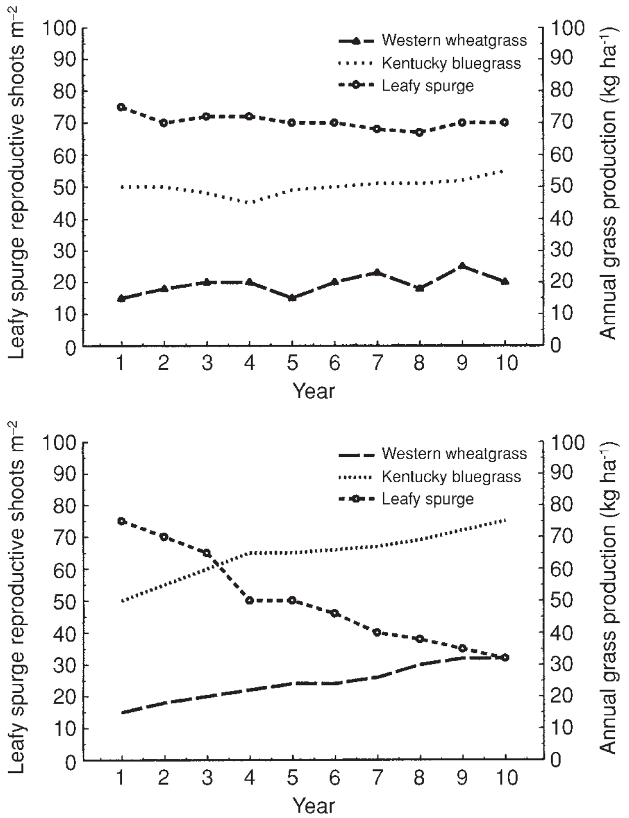

Fig. 10.5. Life-history simulations of western wheatgrass, Kentucky bluegrass and leafy spurge without management (top) and with a shoot-reducing biological control agent (bottom).

For example, Jacobs *et al.* (2000) studied the relationship between *Aphthona nigriscutis* and leafy spurge. *A. nigriscutis*, leafy spurge cover and density, grass cover, forbs other than leafy spurge, litter and bareground were sampled along a transect from the centre of release points (6–8 years after release) to densely infested leafy spurge. Data were analysed using step-down regression procedures, using *A. nigriscutis* density to predict leafy spurge. There was a negative relationship between *A. nigriscutis* density and leafy spurge cover. This relationship is incorporated into the three-species model using the influence of *A. nigriscutis* on leafy spurge to predict the plant community dynamics after imposing the biological control agent. In the future, spatial models must be combined with temporal models to predict landscape-scale changes resulting from management procedures.

Assessing the indirect impacts of biological controls using community dynamics models

Once mechanistic models of plant community dynamics are developed, the predicted resulting plant community or plant community trajectory can be used to determine changes in organization, function and structure. Organization refers to the relative abundance of species and their relationships. Function refers to the various processes that occur in the ecosystem. Structure refers to the type and abundance of organisms in the environment, as well as to its physical features. The indirect impacts of biological controls, or any other management procedures, require predicting species changes and assessing changes in these basic ecological indicators of ecosystem integrity. Risk assessment should include a comparison of the ecological integrity of predicted plant communities without management with those with management.

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11

The Scope and Value of Extensive Ecological Studies in the Broom Biological Control Programme

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Abstract

Biological control programmes have varied in the extent of ecological studies carried out on potential agents and target organisms. At one extreme, studies were limited to surveys for potential biological control agents, which were then shipped to the target country. The biological control programme against Scotch broom (*Cytisus scoparius*) is at the other extreme: we list 29 significant studies on the ecology of broom in its native and introduced ranges, probably representing at least 100 years of work by scientific personnel. These studies have proved useful for predicting the success and safety of the biological control programme against broom as an alien weed. Three studies highlight the significance of insect herbivores reducing broom longevity and seed production: an 11-year insecticide exclusion experiment in the UK; replicated experiments examining recruitment of broom as a native plant in the UK/France and as an alien weed in New Zealand/Australia; and simulation modelling of broom abundance. However, predicting the contribution of each biological control agent to broom suppression is difficult, and may be required for risk–benefit analyses under new regulations. The safety of broom agents to non-target plant species has been addressed using normal host range testing procedures, and extensive field surveys of broom and related plants in Europe. There are concerns over adverse, indirect effects that released

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biological control agents may have on non-target organisms. For insect herbivores released against weeds, adverse indirect effects could occur because the agent acts as a new food source, competitor or disease vector in existing food webs; or because there are adverse effects on existing biota via a reduction in the abundance of the target weed (or non-target plant). Ecological studies of broom enable us to identify some of these potential effects, but predicting their magnitude prior to release of an agent is a major ecological challenge. Equally important to emphasize are the potential benefits to indigenous species from suppression of alien weeds. A balance is needed, because the time and resources required to make accurate ecological predictions of potential adverse effects from released agents could impede biological control of key environmental weeds, resulting in worse net impacts on indigenous species.

Introduction

Classical biological control programmes are nearly always aimed at organisms that have become pests after being introduced into regions beyond their native ranges. Historically, such programmes have varied enormously in the extent of ecological work undertaken prior to, or after, the transfer of natural enemies from the native range into the introduced range of the pest. Programmes aimed at the biological control of weeds in particular have had a long history of safety testing because of concerns that valued economic plants might be at risk. Nevertheless, even in weed biological control programmes, ecological or safety studies undertaken prior to the release of agents have ranged widely in scale.

To illustrate this range we compare two effective biological control agents introduced against the woody shrub, black sage (*Cordia curassavica* (Jacquin) Roemer and Schultes) in Mauritius from 1948 to 1950. The effective insect species were the chrysomelid beetle (*Metrogaleruca obscura* Degeer) and the eurytomid gall wasp (*Eurytoma attiva* Burks). The chrysomelid beetle has external feeding larvae and adults, and both stages were subjected to safety testing using 122 non-target plant species in the beetle's native range in the Caribbean, and 86 non-target plant species after importation into confinement in Mauritius (Simmonds, 1950; Williams, 1951). Three ecological studies were also carried out. The first documented the life history and natural enemies of *M. obscura* in Trinidad (Simmonds, 1950). The second study used simulated herbivory to examine the effect of *M. obscura* on the seed production of *C. curassavica* (Callan, 1948). In the third, field cages were used to show that *M. obscura* was capable of severely defoliating the host plant in the absence of natural enemies, particularly two species of parasitoids (Simmonds, 1948). In contrast, relatively little work was carried out with the gall wasp, *E. attiva*, prior to its release in Mauritius. No safety testing was deemed necessary because 'the insect's mode of development and close adaptation to its host-plant . . . was sufficient guarantee of its host specificity and harmlessness to other plants' (Williams, 1960). Fortunately, this confidence has been borne out, and the insect does appear to have completely restricted its attack to seeds of the intended target weed since it was released in 1949. The weed has been under successful, continuous biological control in Mauritius since the early 1950s (Williams, 1960; Greathead, 1971; Julien and Griffiths, 1998).

Scotch broom, *Cytisus scoparius* L. (Link) (*Fabaceae*), has probably been subjected to a greater level of ecological study than any other plant selected as a target for classical biological control. We review these wide-ranging ecological studies of broom and its associated biota, and then assess how valuable they have been to the biological control programme, particularly with regard to the perceived likelihood of success and the identification and analysis of the risk of non-target effects. First, we introduce the weed and briefly assess the progress made with its biological control.

Scotch broom, *Cytisus scoparius,* as a target for biological control

Scotch broom, henceforth referred to as broom, is a yellow-flowering, leguminous shrub, native to western and northern Europe, which has become an invasive weed in countries such as New Zealand, Australia, Chile, India and the USA. It is a typical target for weed biological control; namely, a plant deliberately transported away from its native range because of its use as an ornamental. The weed is atypical as a biological control target in the huge extent of the ecological studies already undertaken. In most cases, these were not undertaken within a biological control programme. However, large-scale experimental ecological studies have been carried out since 1991 as part of the recent biological control programme against broom run by a consortium of sponsors from New Zealand, Australia and the USA.

Typical problems caused by broom as an invasive alien plant can be illustrated by examining the problems that the plant causes in New Zealand (Syrett, 1987; Jarvis, 1999; Fowler *et al.*, 2000). In South Island hill country in particular, broom is a problem to agriculture because it invades grazing land. It also competes with young trees in commercial plantations. Broom is also invasive on land of significance for conservation, particularly braided river beds and native tussock grassland. Broom is still extending its range in New Zealand, and may affect more such areas or other habitats in the future.

Biological control was first considered for the management of broom as an alien weed in the USA in the 1950s and two agents were released before the programme was terminated, in part because of concerns about potential damage to ornamental legumes (Andres, 1979). New Zealand initiated its own biological control programme against broom in 1981, Australia in 1989 and the USA joined to form a consortium of sponsors in the 1990s. Releases of biological control agents are summarized in Table 11.1. All agents were subjected to extensive testing to assess their host specificity, and hence minimize the risk of attack on non-target plant species after the introduction of the agent into the target country.

In the USA, the seed weevil, *Exapion fuscirostre* F., can destroy 60–90% of seed produced by broom (Isaacson, 1993). The moth *Leucoptera spartifoliella* Hübner causes considerable damage to broom in New Zealand (where it was accidentally introduced, probably in the 1940s), but in the USA its impact is reduced by the presence of one of its parasitoids, accidentally introduced from its native range in Europe (Syrett *et al.*, 1999). It is too early to assess the impact of the deliberate releases of agents in New Zealand and Australia, although *Bruchidius villosus* F. has now reached seed infestation levels of 75% at two sites in New Zealand (Landcare Research, unpublished data). Currently, broom remains an invasive weed in all the countries where biological control has been attempted.

Ecological studies undertaken on broom in its native range in Europe and elsewhere

The insect natural enemies attacking broom in many parts of its native range are well known as a result of over 100 years of entomological study, with 243 phytophagous insect and mite species found associated with broom in Europe (Syrett *et al.*, 1999). This knowledge has underpinned the various classical biological control programmes against broom, and 69 insect species have been considered for use as biological control agents

Table 11.1. A worldwide summary of the deliberate introductions of biological control agents against broom (Julien and Griffiths, 1998; Syrett *et al.*, 1999).

Agent	Modes of feeding	Country introduced into (year first released)
Leucoptera spartifoliella Hübner (Lepidoptera: Lyonetiidae)	Larvae mine young stems	USA (1960 but already accidentally introduced), Australia (1993)
Exapion fuscirostre (F.) (Coleoptera: Apionidae)	Larvae attack seeds. Adults chew buds and flowers	USA (1964)
Bruchidius villosus (F.) (Coleoptera: Chrysomelidae)	Larvae attack seeds. Adults consume pollen	New Zealand (1987), Australia (1995)
Arytainilla spartiophila (Förster) (Homoptera: Psyllidae)	Sap sucking	New Zealand (1993), Australia (1994)

(Syrett *et al.*, 1999). Rather less is known about the pathogens attacking broom in its native range, but some preliminary work has been done on the potential use of two species (*Uromyces sarothamni* Guyot and Massenot, and *Pleiochaeta setosa* (Kirchn.) Hughes) as biological control agents (Syrett *et al.*, 1999).

A large number of studies have been undertaken on the ecology of broom and its natural enemies, and those known to the authors and considered significant are listed in Table 11.2. A detailed research programme investigating broom and its natural enemies was undertaken by Waloff and co-workers at Silwood Park in southern England in the 1950s and 1960s (Waloff, 1968; Waloff and Richards, 1977). This included a range of PhD programmes on components of the broom fauna, pioneering studies on the diets of several predatory species commonly found on broom (e.g. Dempster, 1960, 1963, 1964, 1966) and an 11-year experiment excluding insect herbivores from a broom stand using insecticides (Waloff and Richards, 1977). Recently, the data from much of this work have been elaborated into an analysis of the food web associated with broom (Memmott *et al.*, 2000). Other significant studies include work on the role of broom in succession, where it can encourage the return of native scrub and eventually forest (Williams, 1981). Studies have also shown that in the exotic range, native animal species use broom, including the endemic New Zealand pigeon (*Hemiphaga novaeseelandiae* Gmelin) and a small range of insect species (McEwan, 1978; Syrett, 1993; Syrett *et al.*, 1999).

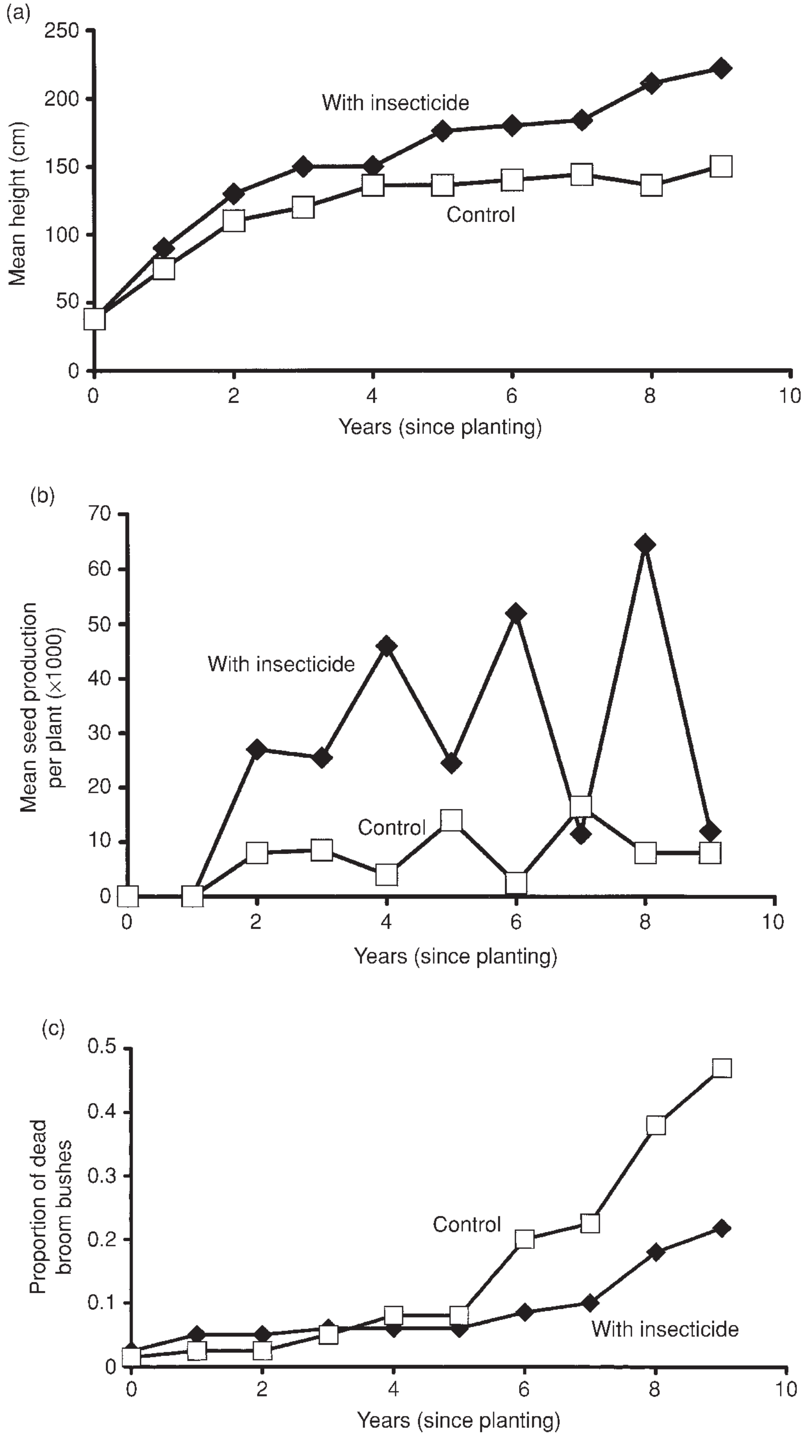
Waloff and Richards (1977) report on a large-scale, but unreplicated, application of insecticides to broom at Silwood Park, UK, for 11 years. Unsprayed bushes: (i) had higher numbers of most insect herbivores in most years (Waloff and Richards, 1977); (ii) did not attain full growth (Fig. 11.1a); (iii) had generally lower annual seed production (Fig. 11.1b); and (iv) had higher mortality compared with the sprayed bushes (Fig. 11.1c). The total seed yield of unsprayed broom was reduced by 75%. However, although these results show a severe impact of insect herbivores on broom plants, seed banks and the recruitment of seedlings into the next generation were not studied, so an impact on the population dynamics of broom cannot be unequivocally demonstrated. From 1991 to 1999, replicated ecological experiments were carried out in the UK, France, Australia and New Zealand to investigate other aspects of the ecology of broom. These experiments examined the size and decay of broom seed banks, intraspecific and interspecific plant competition, natural enemies of seedling broom (vertebrate, invertebrate and fungal), and seed and microsite limitation (by seed-sowing and various cultivation treatments). A simulation model was developed by Rees and Paynter (1997) which showed that the proportion of sites occupied by broom was determined primarily by disturbance rates, the longevity of the broom plants and the probability that broom plants recolonize a site after the original stand senesces (Fig. 11.2a–c). In addition, the model suggests that there are some

Table 11.2. Examples of significant studies of the ecology of broom and/or its natural enemies in (a) its native range, and (b) elsewhere, including studies that compared the plant in its native and introduced ranges.

Authors, including example references (if work published)	Country	Brief note of the nature of the study
(a) Studies of broom within its native range		
Smith (1957)	UK	PhD study on aphids on broom
Dempster (1960, 1963, 1964, 1966)	UK	Studies on the predator–prey interactions of insect herbivores on broom
Parnell (1962)	UK	PhD study on the insects in broom pods
Watmough (1963)	UK	PhD study on psyllids on broom
Danthanarayana (1965)	UK	PhD study on *Sitona regensteinensis* on broom
Williams (1966)	UK	PhD study on *Apion* (including spp. on broom)
Agwu (1967)	UK	PhD study on *Leucoptera spartifoliella* on broom
Singh (1967)	UK	PhD study on *Parthenolecalium* sp. on broom
Waloff (1968)	UK	Studies in the insect fauna of broom 1950s–1968 at Silwood Park
Wall (1970)	UK	PhD on *Chesias* spp. on broom
Waloff and Richards (1977)	UK	Insecticide exclusion trial on broom for 11 years
Noe-Nygaard (1978)	Denmark	Biology of *Apion striatum* Kirby
Hosking (1990)	France, Spain, UK	Surveys of potential biological control agents
Sanz Benito *et al.* (1990)	Spain	Ecological studies of weevils on broom
Hinz (1992)	UK	MSc on broom seed beetles competition and impact
Paynter *et al.* (1998)	France	Ecology of broom using field experiments, 1993–1998
Syrett and Emberson (1997)	France, Spain	Surveys of the host range of broom herbivores in the field
Syrett *et al.* (1999)	Various	Review of potential for biological control of broom
Paynter *et al.* (2000)	UK, France	Ecology of broom, using field experiments, 1991–1996
Memmott *et al.* (2000)	UK	Analysis of the food webs on broom in the UK

(b) Studies including countries outside the native range of broom

Waloff (1966)	USA, Canada	Field surveys on the introduced insects on broom
Williams (1981)	New Zealand	Ecological studies of the role of broom in succession
Waterhouse (1988)	Australia	Ecology of broom
Partridge (1989)	New Zealand	Broom included in soil seed bank and successional studies
Syrett (1993)	New Zealand	Study on the insect fauna on broom
Smith and Harlen (1991), Smith (1994)	Australia	Ecology of broom in Australia: stand dynamics and plant longevity
Bossard and Rejmanek (1994)	USA	Ecology of broom in California: herbivory and competition
Rees and Paynter (1997)	Various	Modelling abundance of broom and the effect of insect herbivores
Downey and Smith (2000)	Australia	Ecology of broom in Australia: long-term stand dynamics
Sheppard *et al*. (2000)	Australia	Ecology of broom using field experiments, 1993–1999
Memmott, J., Syrett, P. and Fowler, S.V. (unpublished results)	New Zealand	Ecology of broom using field experiments, 1993–1999
Sheppard, A.W. (unpublished results)	Australia	Ecology of broom using field experiments, 1993–1999


(a)
Mean height (cm)
250
200
150
100
50
0
With insecticide
Control
0
2
4
6
8
10
Years (since planting)
(b)
Mean seed production per plant (×1000)
70
60
50
40
30
20
10
0
With insecticide
Control
0
2
4
6
8
10
Years (since planting)
(c)
Proportion of dead broom bushes
0.5
0.4
0.3
0.2
0.1
0
Control
With insecticide
0
2
4
6
8
10
Years (since planting)

circumstances (e.g. areas with high levels of disturbance creating a weed population dominated by pre-reproductive plants) in which seed-feeding insects could have significant effects on broom cover.

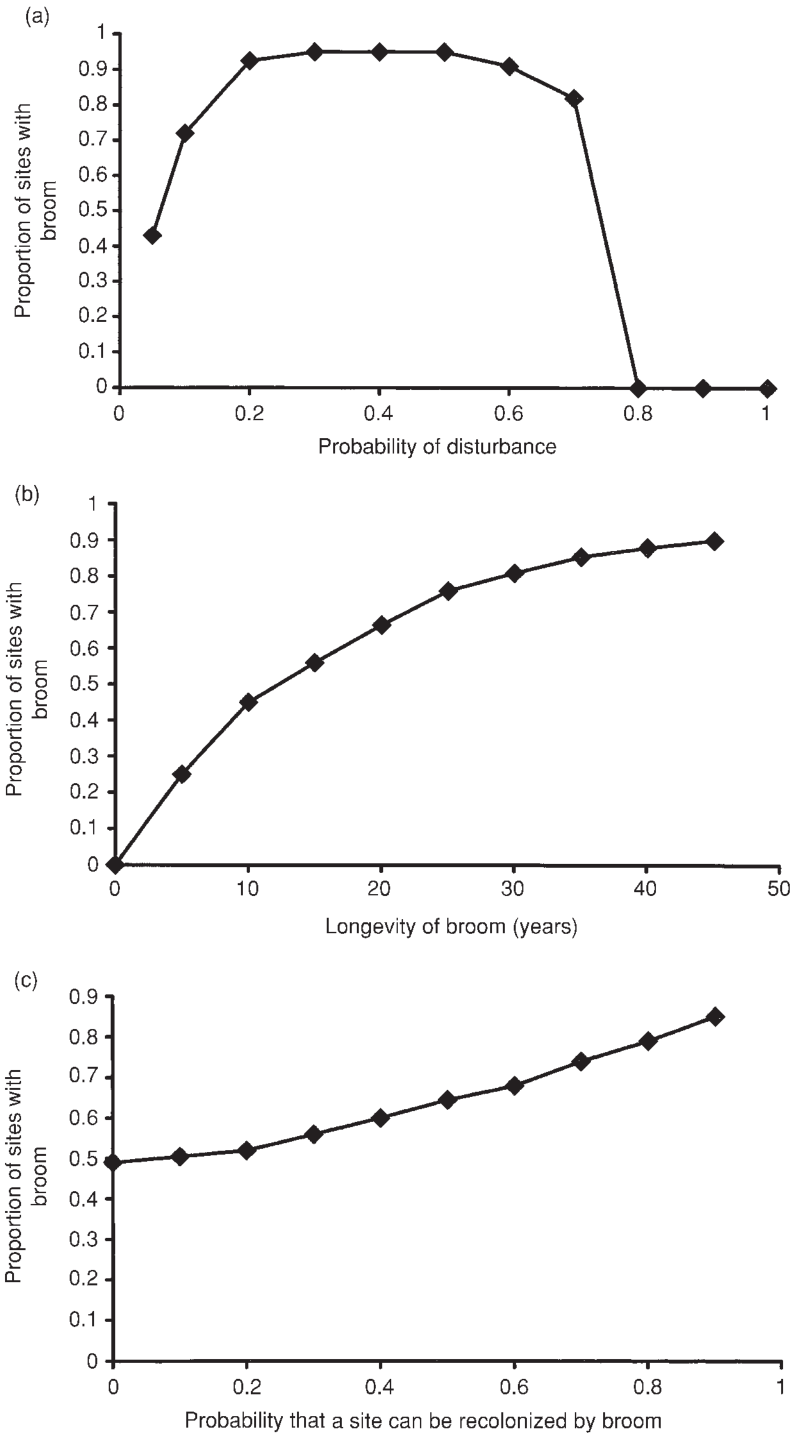
The overall conclusions from the recent ecological studies and modelling can be summarized as follows:

- Moderate levels of disturbance, creating reduced levels of interspecific plant competition are key factors in the creation of broom stands.
- Invertebrate herbivory on broom seedlings in the native range was not significant, but in places vertebrate herbivory caused 100% death of seedlings.
- Modelling indicates that reduced longevity of broom plants could have a major effect on the population dynamics of broom.
- Reducing seed production should reduce the rate of invasion of broom into new habitats, and in some circumstances could affect existing infestations.
- The model highlights the importance of whether broom stands self-replace (as they appear to do in some areas where broom is weedy in New Zealand and Australia, but do only rarely in its native range in Europe).

Overall, these results suggest that the prospects for classical biological control are good. Insect herbivory does reduce longevity of broom in Europe, where broom typically lives for 8–12 years compared with over 20 years in Australia (Smith and Harlen, 1991; Smith, 1994). Seed-feeders should reduce the rate of invasion of broom into new habitats (Paynter *et al.*, 1996), and the model predicts that they could reduce broom cover in frequently disturbed areas such as braided rivers (Rees and Paynter, 1997). Chronic effects of insect herbivores and plant pathogens on broom stands may also allow competing plants, especially perennial grasses, to persist in these stands, and then they can outcompete broom seedlings once the mature broom senesces, preventing a second generation of broom at the site.

Achieving successful suppression of broom using biological control appears feasible provided that sufficient agents are introduced to reduce broom longevity and seed production over all or most of its range as an introduced weed. We now consider whether success in the biological control of broom is likely to result in significant effects other than an amelioration of the broom problem.

Fig. 11.1 (opposite). Summarized results from the 11-year insecticide exclusion experiment at Silwood Park, southern England (Waloff and Richards, 1977). The broom plants from which insects had been partially excluded grew to a greater mean height (a), produced more seed in most years (b), and suffered a lower mortality rate (c).


(a)
Proportion of sites with broom
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Probability of disturbance
(b)
Proportion of sites with broom
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
Longevity of broom (years)
(c)
Proportion of sites with broom
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Probability that a site can be recolonized by broom

The value of ecological studies in predicting the success and safety of biological control of broom

In the modern climate of risk analysis, the prospect of introducing a range of biological control agents to suppress broom raises two general issues. Firstly, as each agent introduction is considered on a case-by-case basis, we are likely to find it necessary to predict the impact that each additional agent will have on the overall aim of the biological control programme. Secondly, the use of more agents probably increases the risk of unwanted side effects from a biological control programme. We discuss these in turn.

Predicting the impact of agents for the biological control of broom

The ecological studies reviewed in the previous section tell us a certain amount about the likely impact of natural enemy species of broom individually. However, substantial uncertainties remain about whether biological control agents will establish and thrive when released into a new environment. One of the most important factors is probably the separation of the prospective biological control agent from predators and parasitoids that normally suppress populations in the native range. Little attention has been given to this in the ecological studies on the broom fauna, probably largely because it has been considered too hard to do. However, the success of at least one potential biological control agent, the gall fly *Hexomyza sarothamni* (Hendel), is dependent on this. *Post hoc* it is comparatively easy to show that, for example, the broom twigminer (*L. spartifoliella*) reaches much higher densities in New Zealand than it normally does in Europe or in the USA, and that this is likely to be due at least in part to the presence of one of the main parasitoid species of *L. spartifoliella* in both Europe (where the parasitoid is native) and the USA (where the parasitoid is an accidental introduction) (Syrett *et al.*, 1999). There is considerable doubt in the biological control community that reliable predictions could be made of the impact of new pairwise associations of a biological control agent and natural enemies present in the region where it has been released. However, in theory, knowledge of the broom insect fauna in Europe and elsewhere should allow predictions of such interactions to be tested both by modelling and by monitoring future releases. Of course, substantial interactions

Fig. 11.2 (opposite). Summarized results from a simulation model developed to predict the spatial distribution and abundance of broom (Rees and Paynter, 1997). The proportion of sites in the spatial model that broom occupies were largely determined by three parameters: the probability of sites being disturbed (a), the longevity of broom (b), and the probability that a broom plant, after senescence, could be replaced by another broom plant (c).

between an introduced biological control agent and an indigenous insect natural enemy fall into one of the categories of indirect and usually unwanted possible side effects of biological control discussed below.

Predicting side effects after the introduction of a biological control agent against broom

Here we restrict our discussion to the potential side effects of a biological control agent for broom on other species and ecosystems, using broom in New Zealand as a model example. For this discussion it is useful to divide these potential impacts into two:

1. Direct effects of the released biological control agent on non-target plant species. This is the possible side effect that the usually extensive host range testing undertaken in biological control programmes against weeds is intended to minimize, or at least predict.

2. Indirect effects of the biological control agent via its presence as a food source, competitor or disease vector, or via its successful reduction in the abundance of the target weed.

Direct effects

Safety in the biological control of weeds has traditionally concentrated on the direct risk to non-target plant species. For this reason, prospective agents are tested against an extensive list of plant species related to the target weed (Wapshere, 1989; Withers *et al.*, 1999). Plants tested in the broom programme in New Zealand have included economically important plants and natives in the *Fabaceae*. The tests are rigorously applied, and otherwise-promising potential agents have been rejected after failing tests. For example, the stem mining weevil, *Pirapion immune* (Kirby), was rejected because of risk of damage to kowhai, an endemic species of *Sophora* in New Zealand (Syrett *et al.*, 1995). Generally, risks to native non-target plant species in New Zealand, from potential biological control agents against broom, are low because there are no native plants in the same tribe as broom (the *Genistae*). The same is not true, however, in the USA, where the genus *Lupinus* (in the tribe *Genistae*) includes a diverse range of native species. Conflicts of interest for biological control of broom in the USA are likely to restrict the agents considered for release there to those showing relatively high degrees of host specificity, such as gall-formers.

In some cases there may be an accepted risk to a non-target plant. In New Zealand, tagasaste (*Chamaecytisus palmensis* (Chirst) Bisby and Nicholls) is an alien plant, with uses in erosion control, as a nursery plant to encourage native species and with potential as a fodder crop (G. Douglas, Palmerston North, New Zealand, personal communication; Jarvis, 1999; Fowler *et al.*, 2000). Tagasaste is closely related to broom, and host range tests show that there is a risk of it being attacked by some prospective biological control agents for broom. If a risk of damage to this alien, non-target plant species is accepted in a decision to release control agents, then there may also be some indirect, or 'knock-on', effects on the native biota. These issues, which are also of significance with broom itself, are discussed further below.

Indirect effects

Indirect effects can also be conveniently divided into those resulting from the agent itself (e.g. as a new food source, as a competitor or as a disease vector) and those arising from the reduction in the abundance of the target weed or of a non-target plant that is attacked. We discuss these in turn, where possible using examples from the broom programme.

Indirect effects on non-target species or ecosystems resulting from the biological control agent itself are most likely to occur if the agent is abundant. Paradoxically then, the most effective agents in biological control programmes might have few such side effects because their populations would be expected to reduce as the target weed was substantially suppressed. The two insect agents released against *C. curassavica* in Mauritius, mentioned previously, are examples where this result may have occurred; both insects became extremely abundant briefly after their release, but are now relatively uncommon, as is the target weed (Williams, 1960; Fowler, unpublished data). Exceptions to this rule, of higher abundance leading to higher risk of indirect effects, might occur if a relatively uncommon introduced biological control agent was capable of efficiently vectoring a plant disease. To some extent these concerns are already addressed in biological control programmes against weeds. For example, the damaging broom aphid *Acyrthosiphon pisum* spp. *spartii* has not been considered seriously as a potential agent because aphids commonly vector plant diseases and are known to probe non-host plants, potentially transmitting viruses or other infectious agents.

In New Zealand, the deliberately introduced biological control agents against broom have not been present for sufficient time to see whether they will be effective or whether they will build up to high populations and still fail to suppress the weed adequately. However, the accidentally introduced twigmining moth *L. spartifoliella* is extremely abundant on broom in many areas of New Zealand. It does suppress the growth and flowering of individual broom bushes (Memmott *et al.*, 1997), and causes mortality of plants in some circumstances (Syrett *et al.*, 1999). Whether the broom problem in New Zealand would be worse still in the absence of this moth is open to debate. The abundance of *L. spartifoliella* clearly makes it a prime candidate for causing indirect effects, such as by acting as a food source for natural enemies. Ecological studies in New Zealand have recorded no indigenous or introduced parasitoids attacking the moth, but little other information on its role as a resource in food webs is available. It is attacked by birds at the pupal stage, and probably by some of the semi-predacious mirid bugs found on broom in New Zealand (H. Harman, Lincoln, New Zealand, 1999, personal communication; Fowler, unpublished observations). The studies on the ecology of *L. spartifoliella* in Europe, and on the ecology of its host plant, do not appear to assist us in assessing potential indirect effects on other species and ecosystems in New Zealand. No effects have been noticed, but it is also true that they have not been searched for systematically. In theory, knowledge of the natural enemies attacking potential biological control agents of broom in the native range could be used to assess whether ecological analogues of these natural enemies exist in New Zealand. Laboratory experiments, in quarantine confinement, could then be used to test whether any of these analogues were capable of attacking the agent prior to release. However, such studies would require considerable resources of money and time, and it is debatable whether the results could be used to make reliable predictions of the outcome of interactions in the field.

The second, broad, category of indirect effects is concerned with effects on species or ecosystems resulting from the biological control agent reducing the population of the target weed (or of other non-target plants, whether predicted or not). Ecological studies in the native range of the weed are probably not relevant to the prediction of these types of effects, but pre-release studies in the target country can help to identify the presence of at least some of these indirect influences of a biological control agent. We could further divide these possible effects into, firstly, those effects resulting from direct usage of the target weed (or affected non-target plant species) by desirable biota and, secondly, the issue of what replaces the successfully suppressed target weed (or non-target plant species). Examples of these interactions, which could occur with successful biological control of broom, are listed below, with comments about whether these are predictable from ecological studies in New Zealand.

A reduction in the range and abundance of broom could have a negative impact on indigenous New Zealand biota in at least three ways:

- The New Zealand native pigeon (*H. novaeseelandiae*) uses both broom and the related alien plant, tagasaste, as a food source in spring and early summer (McEwan, 1978). This has been revealed by ecological studies and by simple observation. Concerns have been expressed by Maori that the native pigeon now depends on broom because native bush has been reduced in many agricultural areas of New Zealand.
- Surveys of the herbivores of broom in New Zealand have revealed that several native insect species utilize the plant (Syrett, 1993).
- Broom, and tagasaste, can encourage the restoration of native vegetation from land where it has been cleared (Williams, 1981; Partridge, 1989; Fowler *et al.*, 2000). The plants can act as nursery vegetation for the establishment of native trees and shrubs and, furthermore, their

attractiveness to frugivorous native birds, such as the New Zealand pigeon, ensures a supply of seed from several important native plant species.

However, predicting the magnitude of these effects is likely to be difficult. In all cases there are other species of plants that can substitute for broom or tagasaste (McEwan, 1978), and in most cases native species would be preferable on ecological and aesthetic grounds. The scenario where successful biological control of broom results in its replacement by alien plants that are even more of a problem does not appear to be likely in New Zealand (P. Williams, Lincoln, New Zealand, 1999, personal communication). However, field experiments where target weeds have been removed by hand have been carried out with hawkweeds (*Hieracium* spp.) and heather (*Calluna vulgaris*). To date, these experiments have not indicated that worse replacement weeds are likely to be a problem.

To summarize, it does seem possible to identify realistic scenarios where adverse effects from the release of broom biological control agents may occur in New Zealand. However, despite the existing ecological studies of broom, it still seems that accurately predicting the magnitude and significance of many of these indirect effects prior to release of the agents is likely to be a major ecological challenge.

Conclusion

The extensive ecological studies carried out on broom and/or its associated biota have shown that the prospects for biological control of broom as an alien weed are good, provided that sufficient, safe control agents can be introduced. With the importance of risk analysis, and the need to balance the potential benefits from a biological control programme against the potential risks, it is clearly vital to be able to demonstrate that there is good evidence for potential success. A challenge probably still remains within the broom biological control programme to demonstrate this potential benefit, in terms of degree of broom suppression expected, for each species of agent for which permission to release is sought.

The potential risks from the introduction of biological control agents against alien weeds have, in the past, often been limited to a consideration of the non-target plants that might be attacked. Typically, the risks to non-target plant species have been assessed using a range of host specificity tests. Surveys of the fauna on broom and related plants in the native range clearly supplement the information from host specificity tests and further reduce the risk of unexpected effects of agents on non-target plant species. More recently, the assessment of other potential non-target effects, both direct and indirect, resulting from the establishment of biological control agents has become necessary. Effectively, this is asking how a biological control agent will fit into an existing food web after it has been introduced, and whether any significant long-term disruption or change will occur. Ecological studies in the native range of the weed can provide useful information here on the nature of the food web from which the potential agent has been 'extracted' for transfer and release in the target country. However, in many cases it is studies of the alien weed and its role (current and predicted, if the weed is still spreading) in the ecosystems of the target country that are more significant. Currently, we believe that making accurate, pre-release predictions of the indirect effects in food webs that are likely to be caused by introduced weed biological control agents will be a major challenge to ecology in terms of:

- how long such studies will take,
- how much they will cost, and
- will they provide reliable, robust predictions?

Although many of the ecological studies of broom listed in Table 11.2 were not aimed at understanding the impacts of potential biological control, it is still a sobering thought that perhaps 100 scientific-personnel–years have been invested in this research. There is also likely to be a public education challenge given that, in countries such as New Zealand, the public is now much more involved with decisions about whether to release new organisms into the environment (Fowler *et al.*, 2000). What has not yet been addressed here is the positive benefit that would accrue to a country such as New Zealand if broom, as an alien weed, could be substantially suppressed. In this case, a recent cost–benefit analysis puts the net annual gain to New Zealand from complete amelioration of broom as a weed at NZ$4–11 million (approximately US$2.5–6.5 million) (Fowler *et al.*, 2000). There would also be benefits to components of the indigenous biota from the suppression of broom in New Zealand, but no monetary value can be attached to these.

While negative ecological effects from biological control agents are clearly unwanted, there is a risk that the time and resources needed to make accurate ecological predictions of these, if actually possible, will cause long delays or even completely obstruct the biological control of important alien weeds. This could not only have consequences in terms of monetary losses to countries, but could also result in worse overall impacts on indigenous biota from the relatively uncontrolled alien weeds. Clearly, there needs to be a balance that takes into account the risks of biological control, as well as the increasing problems, both monetary and conservation-related, caused by alien invasive weeds.

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Index

Figures in **bold** indicate major references.
Figures in *italic* refer to diagrams, photographs and tables.

Acrididae 89, 141
Adalia bipunctata 118, 119
Africa 127–131, 141–143
  cassava green mite 135–136
  cassava mealybug 131–133
  cowpea thrips 137–138
  fungal pathogens against grasshoppers 140–141
  larger grain borer 138–140
  Lepidopterous stem borers 136–137
  mango mealybug 133
  spiralling whitefly 134–135
  water hyacinth 140
agent establishment 27–28, *28*, 132–133, 135–136, 137
agents 3, 4, 28–29, 48, 51, 87, 197–198, *232*
  abundance 241
  diet 71
  fungi *see* fungal pathogens
  generalists 109, 113
  impact of 192, 239–243
  insect 232–233
  parasitoids *see* parasitoids
  predators *see* predators
  single vs. multi-species 9
  specialist 18
  weed control *see* weeds
aggregation 158–159, 168, 169
agriculture
  confidence in safety testing 7–8
  control of insect herbivores 67
  grazing land 231
  non-target problems 64, 66
  safety of biological control 71, 73
  sustainable 100, 114, 130
agroecosystems 100, 113, 120
Agropolis International 2
Aleyrododes spp. 114, 115, 134
alien pests 2–3, 4–5
Amara eurynota 120
America *see* Central America; South America; USA
Anagyrus spp. 132, 133

- Animal and Plant Health Inspection Service (USA) 72, 73
- annual plant life cycle *222*
- ants 197–198
- *Apanteles diatraeae* 108
- Apennine Mountains 153
- aphids 20, 60, 85, 118, 241
- *Apoanagyrus* spp. 132–133
- apparent competition 20, 24, 29, 60–61, 64
- Argentina 218
- arthropods 18, 81–83
  - native communities 68
  - non-target effects of control 40
    - literature reviews 100–102, 102–106, *105*
  - specificity testing 7
  - types of control
    - classical biological 83–86, 87–91, 92–94, 106–109, *108*
    - inundative augmentative releases 86–87, 91–92, 109
- Asia 4, 84, 133
- assembly dynamics 15
- attack rates 19, 22, *22*, *25*, 27, 52
- aubergine 43
- augmentative control 3–4, 5, 83, 86–87, 91–92
  - database 104, 113
  - non-target effects 123
  - severity index *108*, 109
- Australia 43, 64, 85, 148, 201
  - weeds 6, 59, 149, 188, 195, 196, 197, 199
    - broom 231, 232, 233, 237
- Austria 149

- *Bacillus thuringiensis* (Bt) 3, 86, 91
- base-rate effect 192–193, *194*
- bean flower thrips *see* cowpea thrips
- *Beauveria bassiana* (pathogenic fungus) 82, 87, 120, 121
- *Beddingia siricidicola* 85–86
- bees 7, 51
- beetles 7, 70, 84–85, 87, 120, 128, 215, 218, 230
- behavioural assays 48
- *Bemisia* spp. (whiteflies) 4, 114
- Benin 139, 140
- *Bessa remota* 107
- BIOCAT 102, 104, 110
- biodiversity 5, 128, 130–131, 143
- bioinsecticides 86, 120–121
- biological control 2–5, 7–9, 58–59, 140
  - agents *see* agents
  - case studies 113–121
  - history 6–7, 106–107, 113
  - reform of 70–74
- BioNET 130
- Biosafety Protocol 202
- birds 6, 64, 141
- black sage (*Cordia curassavica*) 230
- blackberries 115
- *Brachycaudus cardui* 20
- Brazil 135
- broom biological control programme *see Cytisus scoparius*
- broom twigminer 239
- *Bruchidius villosus* 232
- butterflies 18, 116, 117

- *C. curassavica* 241
- cabbage 115
- CABI, UK 8, 102, 131, 140
- *Cactoblastis cactorum* (moth) 64–65, 73, 198, 199–200
- cactus 65, 200
- cage studies 139, 230
- California, USA 6, 43, 85, 128, 162, 163, 199
- Cameroon 137
- Canada 73, 149, 150, 153, 156, 158, 159, 161
- cane toads (*Bufo marinus*) 6, 64
- cannibalism 61, 119
- carabids 120
- *Carduus* spp. 43, 71, 148, 149–150, 151, 152, 153, 156, 161
- Caribbean, the 63, 64, 65, 134, 230
- carnivores 59
- carp 64
- carrying capacities (prey) 27
- cassava green mite (*Mononychellus tanajoa*) 135–136
- cassava (*Manihot esculenta*) 132, 138, 142

cassava mealybug (*Phenacoccus manihoti*) 131–133
caterpillars 64–65, 87
catfish 64
Catocala ilia 93
cats 64
Ceara rubber (*Manihot glaziovii*) 132
Centaurea spp. 198, 213, 221
Central America 138
Ceransius spp. 137–138
cereals 4–5, 5, 136
CGIAR (Consultative Group for International Agriculture Research) 130
chance 191–192
cheatgrass (*Bromus tectorum*) 221
Chelnidea spp. 198
chemical pest control 2, 3
Chile 231
China 4, 87
Chrysolina spp. 43, 215
chrysomelid beetle (*Metrogaleruca obscura*) 230
CILBA (Complexe International de Lutte Biologique Agropolis) 2
CILSS 140
Cirsium spp. 43, 71, 147–150, *148*, 152–176, 199, 200
clams 64
classical biological control 2–3, 4, 5, 14–15
  arthropods *see* arthropods
  insect agents 83, 138–139
  non-target effects 110–112, *111*
    database conclusions 112–113
    entomopathogens 88–91
    patterns over time 109, *110*
    population changes 100, 106–109, *108*
    severity *105*, 106, *107*
  success of 110–112, *111*
  weeds *see* weeds
climate type 161, 163
climate-matching 135, 193–195
CLIMEX 194
coccinellids 10, 68–69, 119, 132, 134
coconut moth (*Levuana iridescens*) 21
coconuts 84
Code of Conduct for the Import and Release of Exotic Biological Control Agents 8
collateral effects 70, 71
Colombia 135
colonization 30, 213–214, 217–218
Colorado potato beetle 70, 87
commensals 15
commercial biological control 3, 5, 140
common reed (*Phragmites australis*) 117
'community assembly' 14–15
community dynamics 19, 53, 215–225
community modules 16–17, *17*, 32–33, 63
  shared predation *see* shared predation
community openness 28–29
comparative risk analysis (CRA) 188
competition 69, 167–168, 199
  apparent 20, 24, 29, 60–61, 64
competitive displacement 9
competitive exclusion 29
competitive suppression 89
'conflict-of-interest' cases 197, 240
conidia 87
conservation 5, 8–9, 58–59, 83
control agents *see* agents
Convention on Biological Diversity 5
corn rootworm (*Diabrotica virgifera*) 5, 70
cost–benefit analysis 85, 244
costs 142, 203
Cotesia spp. 18, 108
cotton aphids 60
cotton bollworm 70
cottonwood 71
cottony cushion scale 6
cowpea thrips (*Megalurothrips sjostedti*) 137–138
cultivated systems 63, 219
Cyrtobagous 190
Cytisus scoparius (Scotch broom)
  biological control programme 229–232, 243–244
    ecological studies 232–238, *232*, *234–235*, *236*, *238*, 239–243
  see also ecologically based weed management

Dasyurus hallucatus (small quoll possum) 64
data records 102–103, 102–106, *106*
databases 102, 104, 112–113
day length 159
Deladenus siricidicola see Beddingia siricidicola
demography plots 166
density dependence 6, 9, 26, 221
development assistance agencies 5
Diachasmimorpha tryoni 44
Diomus hennesseyi 132
direct interactions 59
dispersal 30, 116, 120–121, 159, 213–214, 217
disturbance 213, 216–217, 233, 237
dose–response assessment 189

ear borers 136–137
Echium spp. 197
ecological effects
  direct 185, 186, *186*, 240–241
  indirect 9–10, 44–54, 166, 185, 186, *186*, 197–198, 240, 241–243
ecological interactions 167–169
ecological risk assessment framework 189–190, *191*
ecological theory 9–10, 100–101, 112
  mathematical models 121–122
ecologically valuable communities 53
ecologically based weed management 211–213
  incorporating biological control 215
  influence on community dynamics 215–221, *216*, *220*
    life history models 221–225, *222*, *223*, *224*
  see also Cytisus scoparius (Scotch broom)
ecology 8–10, 14–15, 89
ecosystems 106–107, 136, 218
  agroecosystems 100, 113, 120
  effect of biological control 8–9, 114
  functional groups 130, 212
  grassland 216, 219, 231
  woodland habitats 138, 139
egg masses 116, 117
egg parasitoids 136–137
egg predation 119
eggs 158, 160, 168
Emex 195, 197
Encarsia spp. 114–115, 134
endoparasitoids 114
endpoint selection *191*
enemy–victim models 27
England 193
entomology 18
entomopathogens 87–88
  classical biological control 88–91
  genetically engineered 92
  inundative augmentative releases 83, 91–92
  non-target effects 87–88, 92–94
Entomophaga spp. 84, 89, 90, 93
Entomophthora shaerosperma 89
Environmental Risk Management Authority (ERMA) 190
epizootics 83, 84, 85, 88, 89, 93
ERBIC 10, 99–102
  case studies 113–114
    exotic generalist parasitoids 116–118
    exotic specialist parasitoids 114–115
    fungi and nematodes as bioinsecticides 120–121
    generalist exotic predators 118–119
  mathematical modelling and ecology 121–122
  retrospective analysis 102–113, *103*, *105*, *107*, *108*, *110*, *111*
establishment 15, 27–28, *28*, 132–133, 135–136, 137
Euglandina rosea (land snail) 57, 65
Europe 100, 113–121, 128–129
European corn borer (*Ostrinia nubilalis*) 87, 116–117
European Plant Protection Organization 8
European Union (EU) 100
eurytomid gall wasp (*Eurytoma attiva*) 230

Eutreta xanthochaeta 44
Everglades World Heritage Park, Florida, USA 59
evolution 31, 45–46
Exochomas spp. 132
expert systems 195
exposure assessment 189, *191*
extinctions
  local 15, 106–107
  non-target prey 6, 18–19, 21, 102, 103, 104, 107–109
  regional 30–31
  resulting from omnivory 60–61
  transient risks 27

facultative pathogens 83
false positives 192–193, *194*
FAO (Food and Agriculture Organization of the United Nations) 8, 127, 128, 131, 134, 141
farmers 129–130
feeding 60, 153, 170, 172, 198
fermentation systems 87
ferns 59
fertilizer 136
field studies 20–21, 93–94, 116–117, 118–119, 152–153, *154–155*
Fiji 21, 107
'Finding of No Significant Impact' (FONSI) 72
Finland 120
fish 63, 64
flies 21, 217
flora, native 66
Florida, USA 64–65, 73, 200
flowerheads 158, 159, 163, 164, 171
food production 129–130, 131
food resources 199
food webs 16, 57–58, 59–63, 67, 131, 132, 233
forest–savannah transition 136
forestry 4, 85–86
forests 84, 136, 142, 218
foxes 64
France 149, 152, 153, 161, 193
fruit flies 9, 44
functional interactions 61–62
fungal pathogens 82–83, 84, 85, 87, 89, 120–121, 140–141
future releases 53–54
fynbos 59

Galerucella spp. 43
gall fly (*Hexomyza sarothamni*) 239
Gallatin Valley, Montana, USA 157, 159
garden plot studies 115, 158–161, 170
Gelis agilis 18
genetic variation 48, 161–163, 171
genetically engineered pathogens 92, 93
geographical range 171–172
Germany 149, 161
Glacier National Park, Montana, USA 213, 216, 217
Global Invasive Species Programme 5
goannas (*Varanus* spp.) 64
golden apple snail (*Pomacea canicularis*) 5
grasses 136, 221
grasshoppers 68, 70, 82, 89, 140–141
grazing 218, 231
Great Plains (N. America) 164–167
'Green Muscle' 141
greenhouse studies 20, 114, 115, 118, 158
greenhouse whitefly 114, 115
growth rate 19–20, 25, 27
growth stages 221
GTZ (Gesellschaft für Technische Zusammenarbeit) 131, 138, 140
gypsy moths 90, 91
Gyranusoidea tebygi 133

habitat finding 48
habitat fragmentation 30, 31
habitats 19, 29, 45, 67, 69, 117
Harmonia axyridis (ladybird) 69, 100, 118–119
Hawaii 44, 65, 107, 108, 128, 134
hawkweeds (*Hieracium* spp.) 243
hazards 187, 188, 189, *191*, 200
heather 243

Heliotropium spp. 198
herbivores 10, 18, 41–42, 59, 62, 66
  insect 67, 164–165, 189, 190, 229, 233, 237, 242
Herpestes javanicus (Indian mongoose) 64
Hesperotettix viridis (grasshopper) 68
Heteropan dolens 107
highlands 136
Homoptera 197
honey production 197
horticulture 4
host
  abundance 132–133
  acceptance 48, 132
  choice of 48, 122, 161
  depletion 91–92
  finding 48
  specificity 6, 93, 117, 132, 170–173, 187, 232
host plants 152, 157, 158
host range
  behavioural studies 50
  evaluation 41–42, 198
  expansion 49, 149, 164, 165
  fungal pathogens 82
  non-target effects 40–41, 87–88, 111–112, 198
  physiological studies 50
  predicting 45–46
  taxonomic limits 7
  testing 42–43, 48–51, 140
host-screening procedures 195–196
human health risks 189–190
human population 129
Hyperaspis spp. 132
Hypericum spp. 43, 193, 199, 215
hyperparasitism 18, 60, 115, 133

IITA (International Institute of Tropical Agriculture) 130, 131, 140
immigration, recurrent 15, 29
impact (ecological) 15, 192, 239–240
India 7, 138, 198, 231
indices of diversity 53
indirect interactions *187*, 198–200, 241–243
  apparent competition *see* apparent competition
  assessing 225
  and evolution 31
  food webs 59–62
  functional 61–62
  host as resource 197–198
  intra-guild predation 60, 69
  landscape scale 19, 28–29
  in natural communities 14, 63
  numerical 61
  self-damping 61
  shared predation *see* shared predation
  transient risks 27–28, *28*
  tri-trophic 62
  trophic cascades 59, 65
indirect mutualism 20, 24
induced resistance 62
inoculation 83, 85
inquilines 18
insect biological control 6, 66
  in Europe *see* ERBIC
insect-vectored plant pathogens 62
insecticides 86, 120–121, 233
insects 83
  introductions 188
  native 66–67
  phytophagous 232
  risks of biological control 66
  safety studies 7
  soil-dwelling 86–87
  surveys 149
integrated pest management (IPM) 1, 2–3, 128
integrated weed management 211–212
Inter-African Phytosanitary Council (IAPSC) 127, 131, 138, 141
interaction webs 63
intermediate levels of control 21–23, *22*, 31
international organizations 131
Internet workshop 40–44
interspecific competition 167–168
intra-guild predation 60, 69, 119
intraspecific interactions 61
inundative releases 83, 86–87, 91–92, 140
  case studies 113–121

  - database 104, 113
  - non-target effects 123
  - severity index *108*, 109

invasive species 15, 192
  - alien 4, 5, 8–9, 73
  - weeds *see* weeds

invertebrates 4, 63
IOBC (International Organization for Biological Control of Noxious Animals and Plants) 2, 7, 8, 10
islands 6, 63, 106–107, 134
isocline predator–prey model 24–26, *25*
Italy 100, 114, 118, 119, 149
itchgrass (*Rottboellia cochinchinensis*) 5
IUCN Red List 204

Japan 84

Kakadu National Park, Northern Territory, Australia 59
Karoo 141
Kentucky bluegrass 219, 221, *223*, 224, *224*
Kenya 137, 139
key factors (population variation) 67
kowhai 240

laboratory testing 50, 93–94, 118–119, 139, 242
lacebugs (*Teleonemia scrupulosa*) 7
lacewing (*Chrysoperla plorabunda*) 20, 60
ladybirds 6, 60, 68–69, 69, 118–119
land-use changes 30, 212
landscape scale effects 15, 19, 27, 28–31
Lantana spp. 7, 44, 198
larger grain borer (*Prostephanus truncatus*) 138–140
larvae 85, 150, 153, 158–159, 170–171, 172–173
latitudinal variation 161
leaf beetles (*Zygogramma bicolorata*) 7
leafminers (*Liriomyza* spp.) 4
leafy spurge (*Euphorbia* spp.) 218, 219, 221, 223–225, *223*, *224*
legislation 3, 5, 64, 71–74, 143, 148, 201–202
legumes 137, 231
Lepidoptera 86, 89–90, 91, 93, 136–137
Leucoptera spartifoliella (moth) 232, 239, 241–242
Levuana iridescens 107, 128
life history 9, 221–225, *222*, *223*, *224*, 230
life table analysis 9, 67
Lissorhoptrus oryzophilus (rice water weevil) 5
literature reviews 101–113
local communities (ecological) 15
local species (as agents) 3, 4
locusts 140–141
Lotka–Volterra model 22, *22*, 29
LUBILOSA 140
lucerne 69, 85
Lydella thompsoni 117
Lymantria dispar 84, 91
Lythrum spp. 43

macrobial agents 3
maize 116, 117, 136, 138
maize borer (*Chilo partellus*) 5
Malacosoma disstria 93
Malaysia 84
management guidelines 74
marsupials 64
mass production (control agents) 84, 85, 87
Mauritania 140
Mauritius 84, 230, 241
meadows 117
mealybugs 132, 133
Mediterranean 153, 161, 162
melaleuca tree 59
Melitaea cinxia 18
melons 115
mesquite (*Prosopus glandulosa*) 70, 71
metapopulation dynamics 30, 41
Metarhizium spp. 120–121, 140
Mexico 73, 138, 139
microbial agents 3, 83, 86, 87, 90, 92
Mimosa pigra 200
Mississippi, river, USA 64, 73
Mississippi, state, USA 64

mites 43, 62, 135
models
  climate-matching 194–195
  ecological 121–122, 189–190
  enemy–victim 27
  life history 221–225, *222*, *223*, *224*
  Lotka-Volterra 22, *22*, 29
  NAS 188–189
  one-predator, two-prey 10
  population dynamics 43
  predator–prey graphical isocline 24–26, *25*
  simulated herbivory 230, 233
  two-predator, one-prey 10
  weed management 215–221, *216*, *220*
molecular markers 48
molluscs 64
mongooses 6
monitoring, risk 188, 203–204
monophagous agents 197–198
Monterey pines 85–86
Montpellier (France), workshop 2, 44–54
Moorea (Pacific island) 65
mortality 6, 9, 102–103, 106, *107*, 159, 160, 168
mosqueta rose (*Rosa rubiginosa*) 218
moths 6, 21, 90, 107, 117, 199, 232, 241–242
multi-species interactions 9, 10, 16
Murgantia histronica 108
mycelia 87
mycetophages 85

NAS model 188–189
native range 190
native species 67–68, 197–198
  as controls 119
  extinctions 106–107, 108, 128
  insects 114–115
  larval parasitoids 117
  protection of 72–73, 128
natural enemies 70
  augmentation of 3–4, 5
  of broom 230, *234–235*, 239
  generalist 10, 19
  introduced 1–2
  shared 18–19
  specialist 10
natural systems 61, 63, 67–68
nature reserves 129
nematodes 83, 85–86, 104, 120–121
Neochetina spp. 140
Neoseiulus idaeus 135
Nephaspis oculata 134
Neptunia spp. 200
Netherlands, The 114, 115, 138
Neurostrota gunniella 200
New Zealand 85, 188, 190, 195, 201
  broom 231, 232, 233, 237, 239, 240, 241, 242, 243
  legislation 148
  thistles 149, 157
nitrogen 136, 218–219
non-biological control 42–43, 52–53
non-occluded virus 84–85
non-target effects 39–41, 241
  assessing 43–44
  classical biological control *see* classical biological control
  density reduction 199–200
  on ecological communities 14–15, 53
  of entomopathogens 87–92
  evaluating 8–9, 46–47, 92–94
  host range *see* host range
  insect biological control 139
    in Europe *see* ERBIC
  internet workshop 40–44
  literature reviews 100–102
  of local biological control agents 4
  patterns over time 109, *110*
  population studies *see* population studies
  predicting 46, 48–49, 240–243
  reducing 47
  relation to control success 110–112, *111*
  severity indices 102, *103*, *105*, *108*, 109
  species selection 47–48
  transient feeding 198
non-target species 46–47
  growth rate when rare 19–20
  impact of predation 26
  regional extinction 30–31

  total mortality 22
numerical indirect interactions 61
nursery vegetation 242
nutrient availability 218–219

obligate pathogens 83, 90
Old World climbing fern 59
omnivory 60, 68
Onopordum spp. 149, 152, 198
Opuntia flora 64–65, 73, 198
organic production systems 3
Orius insidiosis 100, 118–119
overwintering 100, 115, 116, 118, 119, 152
oviposition 85, 92, 136, 153, 156, 158, 159, 162, 170–171, 172, 199

P. melarius 120
Pacific islands 64, 65
Pacific spider mite (*Tetranychus pacificus*) 20
pairwise associations 239
palm rhinoceros beetle (*Oryctes rhinoceros*) 84
parasitism 103, 106, *107*, 116, 117, 137
parasitoids 83, 85, 90–91, 197–198, 239
  exotic generalist 100, 116–118
  exotic specialist 114–115
  indirect impacts 41, 107, 108
  infection with pathogens 88
  native 197–198
  risks of biological control 66–68
  shared predation 18
Parthenium spp. 7, 198
Partula snails 65
patch disturbances 216
pathogens 81–83, 233
  entomopathogens *see* entomopathogens
patterns over time 109, *110*
persistence 109, 111, 168
pest control 6, 83–84, 87–88, 89
pesticides 83, 86, 92
pests 2–3, 4–5, 6, 139
Phenacoccus madeirenis (mealybug) 132
pheromone-baited flight traps 138
phylogeny 195
phytoseiids 135
phytosterols 158
picture wing flies 59
pigeons 233, 242
pine plantations 85
plant community dynamics 213–214, *214*, 225
  controlled colonization 217–218
  controlled species performance 218–219
  designed disturbance 216–217
  life history models 221–225, *222*, *223*, *224*
  successional management 215–216, *216*, 219–221, *220*
plant protection 8, 71–72
pollen beetle (*Meligethes aeneus*) 120
Polynesia 57
Pontederia spp. 140
population dynamics 19, 43, 122
  key factors 67
  reduced longevity 237
  single population 16
  two-species 221
population growth 167, 168, 172
population phenology 152
population reduction (PR) 102, 103, 104, *108*, 109, 242
population studies
  consequences to host plant 198–200
  non-target effects 52, 102–103, 111, 113
    classical biological control 106–109, *108*
post-release studies 166–167
prairie 165
pre-release studies 43, 48–49, 151–156
precautionary principle 202
predation 60, 69, 119
  shared *see* shared predation
predator abundance 19, 22–23, *22*
predator exclusion cages 20
predators 197–198
  general 60, 100
    exotic 118–119
    native 67–68, 197
    risks of biological control 66–68

predators *continued*
  general *continued*
    self-damping 61
  introducing 90–91
  multiple species 61
prediction
  capabilities 9, 48–49, 212–213
  difficulties of 190–193
  impact of agents 239–240
  quantitative ecological effects 173–174
  side effects 240–243
  tools 193–196
predictive capabilities 9, 48–49, 212–213
prevalence *see* base-rate effect
prey species 67
  abundance 19, 26, 27
  alternative 21
  productivity *25*
  range 139–140
prickly pear cactus 6
Propylaea quatuordecimpunctata 119
public involvement 244
public sector research 4, 5
Puccinia carduorum 62

quantitative analysis 101, 102, 113
quarantine 45, 48–49, 131, 138, 242

Rastrococcus invadens 133
rearing cages 119
rearing records 102, 103, 104, 106, *107*
receptor identification *191*
records, data 102–106, *106*
regional dynamics 30–31
regulatory systems *see* legislation
relationship assessment *191*
release application procedures 201
research requirements 101
resource competition 59
response assessment *191*
reticulate food webs 62, 65, 67
retrospective studies 43–44, 51, 53–54, 102–113, *103*, *105*, *107*, *108*, *110*, *111*
Rhine Valley, Germany 149, 152, 171
Rhinocyllus conicus (flowerhead weevil) 43, 148–150, *148*, 199, 200
  ecological effects 167–170, 173–174
  host specificity 170–173
  natural history 150–151
  non-target feeding on *Cirsium* sp. 163–164
  phenotypic and genetic variation, host use 161–163
  post-release studies
    field studies *154–155*, 156–161
    laboratory studies (N. America) 158
  pre-release studies (Europe) 151–152
    field studies 152–153, *154–155*
    laboratory studies 153, 156
  thistle–insect interaction 59, 65, 71, 73
    in prairies 164–167
    tri-trophic 62
  variation in phenology 161
Rhopalosiphum padi (bird-cherry aphid) 20
rice pests 5, 21
Rio de Janeiro, Brazil 128
risk 50–51, 185
  analysis 187–188
  assessment 48, 101, 188
    difficulties of prediction 190–193
    ecological models 189–190, *191*
    NAS (National Academy of Sciences) model 188–189
    prediction tools 193–196
  categories *196*
  characterization 189
  communication 188, 201–203
  comparative risk analysis (CRA) 188
  management 188, 200
  monitoring 188, 203–204
  scenarios 196–200, *196*
  synthesis 204–205

risks of biological control 63–65
  general predators 66–68
  insects 66
  ladybird beetles 68–69
  parasitoids 66–68
  Russian wheat aphid 69–70
  versus benefits 52–53
  weeds 65–66, 148, 185–187, *187*, 196–202, *196*, 243–244
Rodolia cardinalis (ladybird) 6
Rosa rubiginosa (mosqueta rose) 218
row crops 70
rubbervine 199
Rubus spp. 197
Russian wheat aphid (*Diuraphis noxia*) 20, 69–70
rust disease 62
rye (*Secale cereale*) 219

safety 7
  agent diets 71
  ecological 64–65, 128
  of future releases 53–54
  introduced species 73
  restraint 70
  specificity 6
  weed control 71–72, 240
safety testing 7–8, 230
sagebrush steppe 218
Salvinia 190, 192
sampling bias 112
scale insects 9
Scotch broom (*Cytisus scoparius*) *see Cytisus scoparius*
screening 153, 156, 191–192, *194*
searching efficiency 9, 122
seed weevil (*Exapion fuscirostre*) 232
seeds 159, 164, 165, 166, 217, 230–231, 237
selection pressure 160–161
self-damping 61
semi-quantitative analysis 102, 113
Senecio spp. 44
sentinel species 53
sesame 7
severity indices 102, *103*, *105*, *108*, 109
shared predation 16, 18–19
  disparate impacts 19–21
  evaluating risks 31–33
  regional dynamics 30
  transient dynamics 27–28, *28*
shifting landscapes 30–31
shoot-reducing biological control agents *224*
Sicily 118
silkworms 7
Silwood Park, England 233
Silybum spp. 149, 152
sink habitats 29
Sirex noctilio (European woodwasp) 85–86
snails 64, 65
snakeweeds (*Gutierrezia* spp.) 68
soil 159, 219
soil-dwelling organisms 86–87, 104, 106
Solanum spp. 43
source habitats 29, 45
South Africa 43, 59, 89, 140, 201
South America 131, 132, 135
Soviet Union 4
Spain 152
Spalgis lemolea 132
spatial flows 19, 28–29
spatial scales 44
spatial separation 198
spatio-temporal dispersion 51
species maintenance 19
species performance 213, 214, 218–219
species richness 15
species subsets 63
specificity 5, 6–7, 9, 93, 117, 132, 170–173, 187, 232
spillover 29, 31, 132, 167, 168
spiralling whitefly 134–135
spotted knapweed 213, 215, 216, 217, *220*
Steinernema spp. 86–87, 104, 120
stem borers 136–137
stem mining weevil (*Pirapion immune*) 240
storage pests 139
'study type' 103–104, 106
sublethal effects 88
success categories 110–112, *111*
succession 213–214, *214*, 218–219, 233
  management of 215–216, *216*, 219–221, *220*

Sudan 140
sugar cane 3, 64
sugarcane borer (*Diatraea saccharalis*) 108
sunflower 7
surveys 44, 149
sustainable development 4–5
Switzerland 100, 116, 117, 153
synchrony (of flowering) 159, 166

tachnid fly (*Bessa remota*) 21
tagasaste (*Chamaecytisus palmensis*) 240–241, 242, 243
tamarisk 71, 197, 200, 203
Tasmania 85
taxonomic associations (host/enemy) 6
temperate countries 3, 4
temperature, effect of 51, 116, 158, 159
temporal separation 198
Teretrius spp. 138–139
Tettigometra sulphurea 198
Therioaphis trifolii 85
third party species 197
thistles 59, 62, 65, 71, 148–176, 149, 198, 221
three-species model *223*
thrips 87, 118, 137–138
time horizon 44
tobacco whitefly 114
Togo 138, 139
tomatoes 115
trade, problems resulting from 4–5
transect trap experiments 115
transient risks 7
    indirect interactions 27–28, *28*
    shifting landscapes 30–31
transition values 221
transparent sticky traps 116
trap plants 136
tri-trophic interactions 62
Trialeurodes spp. (whiteflies) 114, 115
Trichogramma spp. 100, 116–117
Trichosirocalus horridus (weevil) 62, 71
Trinidad 134, 230
Trioxys complanatus (parasitoid) 85
trophic cascades 59, 65
trophic levels 9, 18, 193
trophic relationships 67–68, 70
trophic spectra 60–61
tropical systems 6, 130, 132
turnip rapeseed 120
two prey species model 23–24, *24*
Typhlodromalus spp. 135
Tyria jacobaeae 44

Uganda 7
uncertainty analysis *191*
United Kingdom (UK) 203
United Nations Conference on the Environment and Development 128
United Nations World Heritage Parks 59
Urophora spp. 217
USA (United States of America) 65
    broom 231, 232, 240
    carp 64
    Department of Agriculture, Agricultural Research Service 39, 156
    imported ladybirds 6, 68–69
    L. dispar 84
    land use 128–129
    legislation 71–72, 201, 202
    national parks 149
    Rhinocyllus conicus see Rhinocyllus conicus
    St John's wort (*Hypericum perforatum*) 215, 218
    tamarisk 71, 197
    thistles 71, 149
USSR, former 87

variance-to-mean ratios 158, 168
vedalia beetles 128
vegetable pests 4
vertebrates 6, 18, 63–64
viruses 84–85

wasps 18, 85, 230
water hyacinth (*Eichhornia crassipes*) 140
weeds 5

- biological control 4, 6, 53, 142
  - broom *see Cytisus scoparius*
  - and ecologically based management 211–225
  - grass carp 64
  - herbivores 41–42
  - risks 65–66
    - analysis 185–187, *187*, 196–202, *196*
    - categories *196*
  - safety 71–72
  - shoot-reducing agents *224*
  - specificity testing 7
  - tamarisk 71
  - United Nations World Heritage Parks 59
  - water hyacinth 142
- weevils 71, 140, 147–176
- West Africa 140
- Western orchard mite (*Metaseiulus occidentalis*) 20
- western wheatgrass *223*, 224–225, *224*
- wheatgrass (*Agropyron smithii*) 221
- whiteflies 4, 114–115, 134–135
- Willamette spider mite (*Eotetranychus willamettei*) 20
- willow fly-catchers 197, 200, 203
- World Food Prize 131

- yellow pan traps 132
- Yugoslavia, former 149

- *Zelus* bugs 60
- *Zoophthora radicans* 85, 89
- *Zygogramma bicolorata* 198