

**Economics of Controlling Invasive Species:**

**The Case of Californian Thistle**

**in New Zealand**

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Dit onderzoek is uitgevoerd binnen *Mansholt Graduate School* of Social Sciences

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**Economics of Controlling Invasive Species:  
The Case of Californian Thistle  
in New Zealand**

Proefschrift

ter verkrijging van de graad van doctor

op gezag van de rector magnificus

van Wageningen Universiteit

Prof.dr. M.J. Kropff,

in het openbaar te verdedigen

op woensdag 25 februari 2009

des namiddags om half twee in de Aula

Economics of controlling invasive species: the case of Californian thistle in New Zealand

PhD-thesis Wageningen University

With reference- with summaries in English and Dutch

Morteza Chalak Haghighi, 2009

ISBN: 978-90-8585-321-3

Invasive species are one of the most significant threats to biodiversity and agricultural production systems leading to huge worldwide economic damages. This thesis has two main aims. The first aim is to analyse the control of an invasive plant in an agricultural system, using the case study of the Californian thistle in New Zealand. The second aim is to study the negative externalities that controlling invasion in agriculture can pose to ecosystems.

To achieve the first aim, both deterministic and stochastic dynamic programming models are set up to find cost effective methods to tackle the problem of Californian thistle. I make a contribution to the literature by performing a dynamic and stochastic programming analysis in which two different categories of control strategies are considered, each with different dynamics. Models are set up with a discrete decision variable consisting of 62 feasible combinations of integrated control strategies. For the second aim I introduce a novel modelling approach in which two compartments are distinguished: a managed compartment where locally a herbivore is introduced to control a weed, and a natural compartment where the same herbivore species can attack a wild plant species. The main processes are herbivory, competition, dispersal and control.

I conclude that bioeconomic modelling is an important tool in analysing optimal management strategies for the control of invasive species and that annual and once and for all choices need to be integrated in the analysis. A stochastic approach is appropriate but does not necessarily lead to different results, depending on the parameter values and the setup of the model. Finally, the method illustrates that an integrated analysis of the economic system and the ecological system is required to assess the risk of extinction of natural plant species. This risk depends on species interactions which in this thesis are competition, dispersal and herbivory. I conclude that a control measure can protect the desirable wild plant species and increase benefits obtained from the ecosystem.

For the policy implications, I conclude that there are several strategies to control invasive species, which can be integrated combinations of control options. The optimal strategy depends on the costs and benefits of the control options. In the case study for the Californian thistle I found that the optimal strategy is a combination of methods. For the interaction between agricultural and natural system I conclude that introducing a biological agent to the agricultural system can cause extinction of a desirable plant in the natural system. The main processes are competition, herbivory and dispersal. These processes are important and need to be analysed in detail before introducing the biological agent. I conclude that the optimal strategy to control the introduced biological agent also depends on interaction of species through competition, dispersal and herbivory.

### **Keywords**

Invasive species, Economics, Californian thistle, New Zealand, Stochastic, Dynamic programming, Biological control, Extinction risk, Herbivory, Dispersal, Competition

To my family, especially,  
To my mother and my brother, Mojtaba  
تقدیم به خانواده ام بویژه  
به مادرم و برادرم مجتبی

Completing a PhD is a long journey which has brought me challenges, great moments and difficulties. Overall I am grateful for the opportunity I had of doing a PhD. It has provided me a great environment to learn at both the professional and personal level and find many friends. I would like to thank all those who supported me in this journey. It is not possible to name all of them therefore I would like to thank all those friends whose names are not mentioned here as well.

I spent the first half of my PhD research at the Economics of Consumers and Households group (ECH) and would like to take this opportunity to express my gratitude to Gerrit Antonides and Wim Heijman for their great understanding and support during this period. Furthermore I extend thanks to the ECH for supporting me with my data collection in New Zealand. I would also like to thank Kees van Kooten for sparking the idea of invasive species management in my mind. My gratitude also goes to Anton Meister for his great hospitality and for providing facilities at Massey University.

My PhD continued to the Environmental Economics and Natural Resources group (ENR) where I spent the second and the most productive part of my PhD studies. Here I learnt many new skills, developed the main part of my thesis, wrote a number of papers and successfully completed my PhD. This would not have been possible without the invaluable support of Ekko van Ierland and Arjan Ruijs, my promoter and co-promoter. I am deeply grateful to Ekko for his useful and wise advice, critical review, understanding, optimism and endless support. Arjan, I truly appreciate your kindness, skilful reviews, comments, and great help in overcoming the challenges and difficulties that I faced during my PhD.

My deep gratitude goes to MSRT, ENR and ECH for their financial support and to Massey University for providing facilities and a valuable network in New Zealand.

I am very grateful to Lia Hemerik for her contribution to chapters 4 and 5, her remarkable feedback and her kind attention despite her busy schedule. My special thanks go to Wopke van der Werf for his valuable comments and inspiring me to find the best way of defining the problem. I am grateful to Eligius Hendrix for providing me with invaluable feedback especially his comments on the mathematical side of my research. Special thank to Elena Saiz for her kindness and great comments regarding programming using MATLAB.

My sincere thanks go to Gareme Bourdôt (Agresearch Palmerston North) and Dave Leathwick (Ag research Linkon) for their co-operation, providing data, and great feedback.

I am very grateful to Gaeme Doole for his comments and feedback at the initial stage of the modelling of my second chapter. Many thanks to El Hadji Fal for being such a good friend, helping with the use of Mathematica and always welcoming useful discussion on the mathematical analysis. Thanks to Clinton Moyoyo who arranged some field trips for me in New Zealand. My special thanks go to Hans Peter Weikard for always welcoming any question or discussion and being a very kind and helpful colleague.

Thanks to all staff at ENR. Especially my great appreciation goes to Wil den Hartog. Her cheerfulness, positive attitude and kindness create a great environment at ENR. Wil, I really appreciate all your support. I also extend my gratitude to staff members at ECH. My special gratitude goes to Annelies Copplemans for being extremely kind, helpful and giving me a hand even when moving to a new house.

I would like to thank all friends and colleagues who I met in the course of my PhD: Guush Berhane, Afaf Rahim, Judith Cornelisse, Kelly de Bruin, Subroto Dutta, Wiepke Wissema, Maarten Punt, Juan-Carlos Altamirano-Cabrera, Hoang Nguyen, Adriana Ignaciuk, Enoch Kikulwe, Petronella Chaminuka, Miyuki Nagashima, Erik Ansink, Kidist Gebreselassie, Diana van Dijk, Karianne de Bruin, Michael Gengenbach, Muyeye Chambray, Zenebe Gebreegziabher for creating a pleasant environment at work and for the nice social activities.

Guush, I am deeply grateful to you. You have been a great, supportive, and inspiring friend since I started my PhD at Wageningen. Thanks for always being there for me. Subroto, I met you for a short period while I was at ECH group. Despite of the short time we created a great friendship, I learnt a lot from your experience and our contact after your graduation and departure did not become shallow. Judith, many thanks for being a great colleague, friend and office mate. You were always nice, positive and helpful with clear idea about life. Kelly, many thanks for your help in proof-reading my papers and translating the summary to Dutch. Afaf, thanks for being a true friend and for all your help in any aspect of my PhD and various interesting discussions. Wiepke, many thanks to you for your great supports, kindness and great Irish sense of humour. Many thanks go to my paranymp, Erik who has been a great gentleman in our PhD group and a very kind person. Maarten, thanks for all the help with the cover page of my thesis and other help regarding Microsoft Office. It has always been nice to have fun and challenging talks with you about the music you play and hearing your stories. I am sure others enjoyed it as well. I like your saying: “one joke a day keeps the doctor away”. Miyuki, Enoch and Diana we had a great exchange of funny conversations after work and indeed I must say that the sense of humour of Diana can be quite competitive. Thanks to Michael for initiating many social dinners at his place and making great dishes.

My special thanks go to Henriette van Strijland, Agnieszka Bucholc, Arjan Wilkens, Babbang Kusomu, Usep Suparman, Cloe Garnache, Katka Severcap, Marina Cherbonnier, Kaka Shahedi, Mehdi Arzanlou, Soleiman Mohammadi, Reza Reyahi and many other friends for their friendship and nice moments which made the PhD process much easier for me. Henriette, you have been a supportive and true friend for me. Your wise and positive approach has been a great example for me. Agnieszka (my paranymp), Arjan and Marina thanks for creating the great moments, fun times and being good friends.

I am grateful to the Iranian community at Wageningen University for organising many social events and being helpful and supportive to me. My special thanks go to Kaka Shahedi Mostafa Karbasioun, Afsaneh Soltani, Ali Talebi, Mohammad Balali and many others.



Sport gave me great strength and energy during the course of PhD. I would like to thank Kishore, Shibu, Anil, Senthil, Abishek, Hadianito and many other friends who created a great and competitive sportive environment at the Bongerd.

I cannot complete the preface without thanking my family. I am very grateful to my parents, brother and sisters for the love that they devoted to me. I especially want to dedicate this book to my brother Mojtaba who I am deeply indebted to for his endless support.



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<b>Chapter 1 General introduction</b>	1
1.1 Introduction	2
1.2 Invasive species in the literature	2
1.2.1 Ecological characteristics of invasive species in pastures	2
1.2.2 Problems of invasive species	3
1.2.3 Control options for invasive plants	4
1.2.4 Costs of invasion	8
1.2.5 Socio-economic aspects of invasion	9
1.2.6 Economics of controlling invasion	10
1.3 Problem definition, objective and research questions	11
1.4 Methodology	12
1.5 The structure of the thesis	14
<b>Chapter 2 Management strategies for an invasive weed: a dynamic programming approach for Californian thistle in New Zealand</b>	17
2.1 Introduction	19
2.2 Material and methods	21
2.2.1 The model of pasture output	21
2.2.2 Dynamics of Californian thistle	22
2.2.3 IWM strategies	23
2.2.4 Optimisation model	27
2.3 Scenarios and results	28
2.3.1 The change in Californian thistle shoot population density under optimal strategies	28
2.3.2 The optimal IWM strategies	30
2.3.3 Optimal path of IWM strategies	31
2.3.4 Optimal trajectory of shoot population density	32
2.3.5 Net present value	33
2.3.6 Sensitivity analysis	35
2.4 Summary and conclusions	36
<b>Chapter 3 Biological control of invasive plant species: a stochastic analysis</b>	39
3.1 Introduction	41
3.2 Case study: Californian thistle in New Zealand	42
3.3 Model	43
3.3.1 A Deterministic dynamic programming model	44
3.3.2 The Stochastic dynamic programming model	46
3.3.3 Probability distributions for the weevil and mycoherbicides efficacy	49
3.4 Results and Discussion	52
3.4.1 Transition of the thistle density between year $t$ and year $t+1$	53

3.4.2 Optimal Strategies	54
3.4.3 Sensitivity	57
3.5 Implication of results for management of the thistle	58
<b>Chapter 4 On the risk of extinction of a wild plant species through spillover of a biological control agent: analysis of an ecosystem compartment model</b>	65
4.1 Introduction	67
4.2 Description of the model system	68
4.3 Mathematical analysis	71
4.4. Numerical analysis	74
4.5. Discussion	80
4.6. Conclusions	81
<b>Chapter 5 Invasive species: economic analysis of dispersal, plant competition and herbivory</b>	85
5.1. Introduction	87
5.2. Description of the bioeconomic model system	88
5.2.1 Ecological system	90
5.2.2 The economic system	92
5.3. Numerical analysis	94
5.4. Conclusions	103
<b>Chapter 6 Discussion and conclusions</b>	105
6.1 Introduction	106
6.2 Answers to the research questions	106
6.3 Conclusions	109
6.4 Suggestions for future research	113
<b>Summary</b>	127
<b>Samenvatting</b>	133
<b>Curriculum Vitae</b>	139
<b>Completed Training and Supervision Plan</b>	141

## Introduction

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## **1.1 Introduction**

Invasive species are one of the most significant threats to biodiversity and agricultural production systems. The majority of our natural ecosystems suffer from invasive species. Alien weeds are the most costly invasive species leading to huge worldwide economic damages (Sheppard et al. 2003). Production losses due to invasion and costs of controlling invasion generate large economic damages. There are many ways of controlling invasive species, and some of them can cause negative externalities.

This thesis focuses on the problem of invasive species management in agricultural systems and possible spillover effects to ecosystems. I focus on modelling these issues in three settings: 1) a deterministic setting 2) a stochastic setting, and 3) a setting of a two compartment model. For the first two settings, I tackle the problem of invasion of Californian thistle in pastures in New Zealand and study various methods to control it. This provides a novel approach to deal with the complex interaction between human activities and ecological processes. The third setting, uses a complex and novel approach by looking at a two compartment system. This setting combines an analytical approach with a numerical analysis, and loosely presents the example of Californian thistle in the managed compartment and the surrounding ecosystems in the natural compartment. It first finds how intervention in the managed compartment can threaten biodiversity in the natural compartment based on an ecological model. In the same setting, a bioeconomic model is developed to find an optimal manner to manage a biological control agent, that may cause damage to ecosystems.

## **1.2 Invasive species in the literature**

Invasive species are defined, as species that are non-native to the ecosystem and whose introduction causes or is likely to cause economic or environmental harm (Weber 2003). Their characteristics and in particular their ability to spread, are some of the reasons that make invasive species a problem all over the world. Management of the problem of invasive species requires understanding their characteristics. This section focuses on common characteristics of invasive plant species, the problem these species cause, methods to control them and costs of control.

### **1.2.1 Ecological characteristics of invasive species in pastures**

Invasive plants are able to adapt themselves to the new environmental conditions of a site (Wagner 1991; Weber 2003). It means that invasive plants have some characteristics that make them adaptable and more competitive than native plants. There are many physiological characteristics that make invasive plants successful in tolerating conditions of a new environment (Tyser and Key 1998). For example: lack of palatability (i.e. the potentiality of

the plant being grazed by animals), high seed germination, tolerance to defoliation, and allelopathy. The *lack of palatability* of invasive plants helps them to compete better with palatable species which are heavily grazed by animals.

*Seed germination* is a very important factor for establishment of plants. In many pastures, early drought and heavy grazing contribute to reducing seed germination of plants. Seeds of invasive plants often can better tolerate harsh environmental conditions and germinate under more difficult condition than seeds of many native plant species. This makes invasive plants more competitive under harsh environmental conditions. As a result, overexploitation and severe environmental conditions can have more negative effects on the native species than invasive species. This facilitates invasive species to germinate and establish. For example seeds of *Serrated tussock* which is a major economic problem in Australia can survive up to 13 years in the soil (Vere and Campbell 1984).

*Defoliation* caused by grazing often reduces root growth of palatable plants (Lacey et al. 1990) and has less effect on invaders, which are unpalatable. This would reduce the competitiveness of the palatable plant in relation to the invasive species, encouraging the establishment and growth of invasive species (Vere and Campbell 1984; Dahl et al. 1989; Lacey et al. 1990). Thus, invasive species can easily invade over-grazed rangelands.

*Allelopathy* is about chemical interaction between plants. From the beginning of this century evidence has accumulated that plants may, directly or indirectly, harm each other through release of chemicals to the environment (Rice 1974). This chemical interaction (Allelopathy) includes stimulatory as well as inhibitory influences (Putnam and Tang 1986). Many invasive plants are allelopathic. Californian thistle, for instance, is an invasive plant that produces a phytotoxic substance from the root and foliage, which makes establishment of native plants difficult (Bendall 1975).

These characteristics that facilitate the arrival and establishment of invasive plants are important when considering efficient management policies.

### 1.2.2 Problems of invasive species

Many of the ecological problems that exist in rangelands, forests, golf courses, parks, fishing and boating sites originate from the introduction of invasive plants (Monaco et al. 2001; Adams and Lee 2007). Invasive plants cause many ecological problems such as lower plant and animal yield, health problems, less efficient land use, higher costs of pest and plant disease control, more water management problems, and lower human efficiency (Tyser and Key 1988; Lacey et al. 1989; MacLeod and McIvor 2008). To have a better understanding of the problems that invasive plants impose on the invaded area, the problems are categorized into three categories: ecological impact, yield impact and externalities. Each category is closely connected to the others. In this thesis, the following impacts will be tackled.

a) Ecological impact. Invasive plants can have several ecological impacts on the environment. Invaders affect the native fauna and flora. They compete with native plants for resources; especially space, nutrient, water and light. Their competitiveness changes the quantity of resources that is available for native species. They even replace desired native plants and prevent the native plants from establishing because of their superior competitive ability (Buchanan 2000). For example in California and Arizona, perennial native and palatable plants lost competitiveness and invasive plants have become dominant (Bridges 1992). Diffuse knapweed is an example of an invasive plant that prevents the growth of native species (Fletcher and Renney 1963; Muir and Majak 1983), altering yields in agriculture.

b) Yield impact. Competition between native and invasive plants in absorbing resources can reduce farm plant yield (Buchanan 2000; Monaco et al. 2001). In the USA, weeds reduce agricultural yield by 12%, which cause approximately a loss of \$32 billion crop value annually, for a potential crop value of more than \$267 billion per year (Pimentel et al. 2000a). Diffuse knapweed, for instance, has reduced forage production over a million hectares of rangeland in the western United States (Watson and Renney 1974; Myers and Berube 1983; Tyser and Key 1988; Lacey et al. 1989; Sheley et al. 1997). Research on sandy rangeland in western Texas shows that even modest weed invasion reduces usable forage by 560-785 kg/ha (Dahl et al. 1989). The cost of invasive plants to crop systems in Australia has been estimated to be AU\$1.271 billion annually. Invasion of weeds leaves the invaded area unused by livestock and even if livestock graze them, it can negatively affect animal body weight, because the grazing value of invasive weeds is usually low due to their low protein and high fiber content. For example grazing *Serrated tussock* can reduce the body weight of animals because of its low grazing value (Campbell and Barkus 1966). Livestock can be poisoned or even killed if they graze some invasive plants.

c) Externalities. The effort of environmental managers to control invasive plants in agricultural systems by biological agents can cause externalities to the natural habitat due to their spillover effects (Rand et al. 2006). Thus the biological agent can spillover from the agricultural land to a natural habitat and target some desirable wild species. In this way, the biological agent acts as an invasive species in the natural land and produces negative ecological and yield impact and can cause economic losses.

### 1.2.3 Control options for invasive plants

There are different ways of dealing with invasive species. I present some of those options and highlight their positive and negative aspects.

**Biological control.** Biological control is the use of natural means to control unwanted plants. Plant competition, insects, and pathogens are some examples of biological control that will be explained here.



1. **Plant competition:** Competition among plants in the environment is an important factor that influences plant-plant interactions. Plants compete for space, light, water and nutrients in the soil. Plant competition has been used to complement other invasive species control methods (Bottoms et al. 1995). For example, some invasive species like Russian knapweed are sensitive to light shortage, therefore plant competition that reduces the amount of light can be used to control those invaders (Latterra 1997).

2. **Insects:** insects are used to control the growth of a specific plant species. The insects usually come from the native habitat of the invasive plant and should be tested extensively to ensure that they will not attack plants others than those being targeted (Kennedy, 1999). Insects, once established, can often support their own growth and expansion.

3. **Pathogens:** Pathogens are small organisms, such as viruses or bacteria that can cause disease. Pathogens are used for controlling invasive plant species. Extensive research is being conducted on many fungal pathogens and bacterial biological control agents, as summarized by Kennedy (1999). Many have shown good potential for the management of some invasive plant species.

The advantage of biological control is that little energy input is required for control once established and that they are very cost effective (Hill and Greathead 2000). The worst case scenario with biological control, however, is that they may not succeed in eliminating the target invaders, and/or may spread into the local biota and damage local treasured species (Simberloff and Stiling 1998; Crooks 2005). Biological control is a long-term control technique that will not always solve invasion problems quickly. Moreover, invasive plants can develop resistance to biological control agents. These might be considered a disadvantage of this method (Giga et al. 1991; Ortiz et al. 1995; Derera et al. 2000).

**Chemical control.** Chemical control involves the spraying of synthetic products. Herbicides are one of the most effective ways of managing invasive plants in the short term and can be important in increasing the production on rangelands (Barrons 1969). Herbicides can give the best result in combination with other methods. Morrow and McCarty (1976), for instance, concluded that herbicides and fertilizers can be effectively combined to increase pasture production.

Some of the advantages of this method are its high effectiveness and low labour requirements. Benz et al. (1999) concluded that herbicides control Russian knapweed more effectively than mechanical measures. Chemicals, however, have disadvantages. Today they are considered as controversial and environmentally unfriendly (Vurro and Jonathan 2006; Sexton et al. 2007). They can pollute nature, affect wild life, and damage animals and human health (Monaco 2001). Beside having negative environmental impacts, chemicals can become ineffective when invasive plant become resistant to them (Charudattan 2001; Llewellyn et al. 2007).

**Mechanical control.** One of the most common types of mechanical control is mowing. The advantage of mechanical control is both in economic and ecological terms: on the one hand it

has low costs and on the other hand it reduces the need for environmentally unfriendly methods such as chemicals (Astrand and Baerveldt 2001). Political interests also increases the use of mechanical control by farmers. The European Union, for instance, has decided to increase organic farming methods. Here, the market also plays an important role. Nowadays, farmers are more attracted to mechanical control because of increasing demand for organic farming (Astrand and Baerveldt 2002). Mechanical control can cause soil erosion and reduce soil fertility (Farquharson et al. 2008). Next to that, it is not always possible to apply this method since it requires a good soil-water relationship, that is not always available in rangelands (Buchanan 2000).

**Intensified grazing.** Grazing animals such as geese, goats, sheep and cattle have been used to control invasive species in rangelands. Sheep and goats are most commonly used for this purpose because they often eat plants that are rejected by cattle and horses (Popay and Field 1996). Geese are specialized for control of small seedling grass weeds. Animals will eat plants at specific stages of plant growth, so it is important to be informed about what animal is the best agent at different times of the year. The negative effect of grazing invasive plant on the body weight of animal is considered as one of the costs involved with this method. This method is environmental friendly and has low costs. One of the disadvantage of this method, however, is that it can be less effective than other control methods such as chemicals (Popay and Field 1996). This method is also not applicable if the invasive plant is poisonous to animals.

**Prescribed Burning.** Burning is another way of controlling invasive species. In this method farmers burn the pasture. Fire can help the native plants to take over the pasture and stop invasive plants to re-grow after burning. It means that burning should damage the invasive plant but not the native plants. Therefore the time of burning is a very important issue and burning at different times of the year gives different results. Burning after flowering of native plants and before flowering of the invasive plants gives the best result, because burning at this stage prevents invasive plant to produce seed while native plant could produce more seeds, which increases the competitiveness of native plants against invasive plants (Engle and Stritzke 1992).

The advantage of burning is that it can easily destroy invasive plant seeds and stimulate germination of native plants, in this way increasing biodiversity (Kruger 1983). Burning can be economically feasible across a wide range of economic and environmental conditions (Johnson et al. 1999). However, this method is highly controversial. Public safety, the risk of escape, decreased aesthetics, inconvenience from smoke and CO<sub>2</sub> emission, fiscal responsibility, reduced soil and air quality are some of the primary reasons that make this method unattractive (Bååth et al. 1995; Hesseln 2000).

**Combination of different control treatments.** Different control options can be combined. An integrated weed management (IWM) approach that emphasises the use of several control measures is suggested to be the most effective way of controlling invasive weeds (Miller et al. 1992; Christianson et al. 1994; Ferrell et al. 1993; Buckley et al. 2004). Biesboer et al. (1993) concluded that the combination of herbicides, seeding, and fertilizer use can be best to deal with leafy spurge in the long-term.

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***Text box 1.1 The case of the Californian Thistle in New Zealand.***

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*New Zealand is a country with a very diverse and valuable natural resources base. Today New Zealand ranks among the highest invaded areas in the world. There are about 2000 native species and 1800 invasive plants in New Zealand (Williams and Timmins 2002). Many of the native species in New Zealand are unique and need protection from invasive species (Walker et al. 2006; Dymond et al. 2008). Most of 140 species that are used for forestry, agriculture and horticulture in New Zealand are introduced (Pimentel 2002b). About 200 of the invasive plant species have become harsh weeds that cost about NZ\$60 million annually to control. Additionally damages of invasive weeds to crops are estimated to be NZ\$40 million per year (Pimentel 2002a). Many weeds impede pastoral farming in New Zealand and one of the most important of these is Californian thistle (*Cirsium arvense*), a perennial which is widely distributed. It is found in both perennial and annual crops in Eurasia, America and New Zealand and is called one of the “world’s worst weeds” (Holm et al. 1977).*

*Californian thistle is a very troublesome weed because it is more difficult to control than other invasive plants (Hakansson 1969; Kvist and Hakansson 1985). The root of the Californian thistle reaches deep into the soil (Nadeau 1988). Hence, part of the root system can escape the disturbance caused by tillage (Donald 1994). Nadeau and Vanden (1990) found the main part of the regenerative roots down to depth of 40 cm. It makes this plant also resistant to harsh environmental conditions.*

*In New Zealand, Californian thistle occurs in pastures and crops where population increase occurs by recruitment of adventitious shoots from the creeping root system, and by establishment of seedlings on open land (Cockayne 1917; Bascand and Jwett 1982; Bourdôt and Kelly 1986; Bourdôt et al. 1995). Californian thistle is a big problem as it restricts the area available for grazing livestock and reduces the plants’ yield (Donald 1990). O’Sullivan et al. (1982 and 1985) showed that a density of 20 Californian thistle shoot/m<sup>2</sup> significantly could reduce crop yields by 26 to 51%. Despite cultivation, herbicides and grazing, Californian thistle has been rarely adequately controlled (Hartley and Butler 1984; Hartley et al. 1984; Meeklah and Mitchell 1984). Control of the thistle by herbicides and mowing costs NZ\$27 million per annum, including costs of vaccination for scabby mouth disease in*

*sheep in the heavily infested Southland and Otago regions in New Zealand. This cost is promoted by wounds around the mouths of grazing animals caused by the thistle's spines (Gourlay 2004). The total annual cost of the Californian thistle to New Zealand pastures, through both the cost of control and losses related to pasture production, has not been estimated but will greatly exceed this value (Bourdôt et al. 2005). Despite the fact that many control techniques have been applied to control this plant, there is a question that has not been answered: What are the best IWM strategies for controlling this plant?*

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#### **1.2.4 Costs of invasion**

Damages of invasive species as well as their control costs are large. Two estimates of the total cost of invasive species at the national level relate to the United States. In 1993, the Office of Technology Assessment (OTA) estimated damage costs of 79 harmful species to be \$97 billion per annum. After seven years, the costs of invasive species for a wider number of invasive species have been estimated to be \$137 billion annually (Pimentel et al. 2000; Perrings et al. 2002). Even the second estimate could be an underestimate, because it included only a subset of the invasive species impacts (Perrings et al. 2002). Also in Australia, invasive weeds heavily infect the ecosystem and cause AU\$1.271 billion of annual damages to the crop systems. In addition, damages to pasture and horticultures are estimated to be AU\$494 and AU\$213 million, respectively (Pimentel 2002a).

Production losses due to invasive plants can be huge. In New South Wales, serrated tussock caused a AU\$11.8 million loss in terms of forage on Merino wool production enterprises in 1976-1977. This loss was equivalent to 31% of the value of merino wool produced in New South Wales (Vere and Campbell 1979). Weeds, as invasive plants, reduce cultivated area by 12% annually and increase costs by the same amount in South West of the United States (Pimentel et al. 2000). On the British Isles, invasive species damages and control costs are estimated to be £200-300 million. In India, exogenous plants are responsible for a 20% crop loss. In Brazil, their costs are estimated to be \$69 billion annually. In South Africa, pest weeds in the mountain fynbos area cost \$11.8 billion, in reduced stream flow \$1.4 billion, and in water fern impact in aquatic ecosystem \$58 million (Pimentel 2002b). Generally the replacement of perennial grass species by weeds imposes costs to the pasture by reducing the productivity (Vere et al. 1993; Jones and Dowling 2005). These studies show that on a global level, invasive species costs are large.

The costs of control techniques can be substantial as well. Estimating these costs is very important in assessing the feasibility of invasion management. The control costs of *Nassella trichotoma*, *Hypericum perforatum*, and *Cassinia arcuata* in rangeland in Southeastern Australia have been estimated to be AU\$122 per hectare (Campbell 1977). Costs of controlling invasive plants by MCPA and mycoherbicides is estimated to be around NZ\$115

per hectare in New Zealand (Burt 2004). Weed management by chemicals near Pullman (WA, United States) varies between \$12-76/ha per year (Kwon 1995). Costs of controlling scotch broom in the National Park of Australia has been estimated to be AU\$15000 for manual pull, AU\$45000 for herbicides, AU\$ 76848 for biological control and AU\$15000 for grazing animals per year (Odom et al. 2003). Control costs can be related to the number and or size of endangered areas, and with the number of endangered plant species. For example in Australian agricultural, area control costs increased by about AU\$5800 per year for each additional endangered special conservation area (Sinden and Griffith 2007). Literature presented above shows that the costs associated with invasive species as well as their control are large. Thus it is crucial to control invasive species in an effective and sustainable manner.

With the high costs of invasion, successful control of invasive species in heavily infested land area requires high expenditure (Vere and Campbell 1977). As a result, landholder opportunity cost of capital is an important factor in the decision to control invasive species. Landholders who are already in debt or cannot raise a large amount of capital will have difficulties to control invasive species. For example, in 1976, as a direct result of a *Nassella trichotoma* invasion, 34 landholders in Cookwellshire in southeastern New South Wales were forced to obtain off-farm work to raise the necessary capital for control (Campbell 1977).

### **1.2.5 Socio-economic aspects of invasion**

The economic literature has studied a vast range of economic and social aspects of invasive species. Invasion through (international) trade (e.g. Horan 2005a and 2005b; Jones and Corona 2008), government policies related to invasion (e.g. McAusland and Costello 2004; Costello et al. 2007) and effects of market based instruments (Horan 1998; Gren 2008; Jones and Corona 2008) are some examples of social and economic aspects of invasion that have been studied. For example Perrings et al. (2002) argued that the dependence of the economy on trade and transportation paths, demographic patterns, and the economic roles of invasive species and their competitors and predators are important factors that influence invasion. These factors can depend on government policies and relative prices. The market prices of species that can be potentially invasive do not include the costs of invasion that they may cause. Thus, the negative effects of invasion are external to the market. In some cases, ecosystems have become more vulnerable to invasions due to price, tax, and incomes policies (Genovesi 2000). For example, subsidies have reduced plant diversity by supporting export of crops and increasing the use of pesticides which reduce the resistance of ecosystems to invasions. Moreover, property rights regimes also can have negative influences on the concerns and action against invasive species. Also encouraging trade through the liberalization of regulations has increased trade and consequently increases the spread of invasive species. Perrings et al. (2002) argued that adaptation of human behaviour and social norms have been slow to react to the new risks and consequently have increased invasions.

The focus of this thesis, however, is not on these general economic aspects. This thesis focuses particularly on the control of an invasive species in an agricultural system and introduction of a biological agent that can affect the rest of the ecosystem.

### **1.2.6 Economics of controlling invasion**

There are several studies on the economic feasibility of controlling weeds using net present value (NPV) and benefit-cost ratio investment criteria (Nielsen and Cronin 1977; Vere and Campbell 1984; Headley 1985; CRC 2001; McConnachie et al. 2003). Not all cost-benefit analyses fully capture the population dynamics. To find the optimal management strategy, given the dynamic character of their populations, a dynamic analysis is required in which net present value (NPV) of the agricultural activities over time is maximised. In order to analyse the effect of population dynamics of invasive species on the optimal measures of control, dynamic optimisation methods are often applied. White and Wadsworth (1994), for instance, used a dynamic optimisation approach to find the optimal management practices for livestock grazers and harvesting grouse. Their approach maximises the net return obtained from the pasture. The same approach has been used for management of plant invasion by Kennedy (1987); Higgins et al. (1997); Wu (2001) and Odom et al. (2003) and Jones et al. (2006); and for finding optimal harvesting regimes by Bulte and van Kooten (1999). Some control options introduced to control invasion can have an irreversible effect, however. For instance, once introduced some biological agents will remain active in the environment forever. A comprehensive study is needed that distinguishes between reversible and irreversible control treatments and that combines them in a single dynamic optimisation framework .

The deterministic dynamic optimisation approach does not always provide the best results. Some of the elements used in optimisation models, such as the efficacy of control options and population dynamics, can be subject to stochasticity. This is caused by changes in environmental conditions and difficulties to establish in the new environment. In this case, a stochastic dynamic optimisation model that captures the stochastic elements of the model can provide better results. Several studies use stochastic optimisation models, like Bulte and van Kooten (1999), Pandey and Medd (1991), Cacho et al. (2008). For the case in which there are irreversible effects of control measures, a stochastic analysis is required that looks at combining a number of reversible and irreversible control strategies.

Controlling invasive species can have unintentional negative effects on the neighbouring sites. In this way, introducing a control agent in one site can have external effects on other sites. For example, biological control agents that are considered as a safe and cost effective means of controlling invasive plants (e.g. Hill and Greathead 2000) can penetrate to remote native habitats and feed on alternative host plants in natural habitats (Symondson et al. 2002; Rand et al. 2006; Wirth et al. 2007). These biological agents can produce large negative effects in the natural habitats by their spillover or cross-edge invasion effects (Suarez et al.

1998; Cronin and Reeve 2005; Rand et al. 2006). A systematic analysis is needed on the ecological characteristics of these negative effects and of an optimal management strategy from an economic and ecological perspective.

### 1.3 Problem definition, objective and research questions

Recognising the costs and negative effects of invasive species to the environment and the importance of controlling them, it is important to find cost effective control strategies to deal with invasion. This thesis has two main aims. The first aim is to analyse the control of an invasive plant in an agricultural system. As a case study I use the Californian thistle in New Zealand, in order to assist farmers in New Zealand to find the most cost effective strategies for controlling Californian thistle in their pastures. For this purpose I develop models that enable systematic analysis of the thistle and I introduce some new elements in the models, which have not been covered by previous studies. In this way, this thesis contributes to the modelling of invasive species control. The second aim of this thesis is to study the negative externalities that controlling invasion in agriculture can pose to ecosystems. To reach the aims of this thesis, the following research questions are raised.

*Q1 What is the best modelling approach to tackle the problem of Californian thistle and what are the most cost effective strategies to control it?*

To tackle the problem of Californian thistle in New Zealand several control options are available. In this thesis, integrated weed management strategies are considered that combines 4-chloro-2-methylphenoxy (MCPA), 4-(4-chloro-2-methylphenoxy) (MCPB), intensified grazing, mycoherbicides, mowing in January and mowing in March and introduction of the insect (*Apion Onopordi*). Combining these seven control options gives 62 feasible IWM strategies. A deterministic, dynamic programming model is developed to study the most cost effective IWM strategies.

*Q2 How to model the problem of Californian thistle when some control options have stochastic effects and which are the best control options under a stochastic setting?*

IWM strategies that include the introduction biological control agents can have stochastic effects on the Californian thistle. This thesis accounts for stochasticity by developing a stochastic optimisation model to find the most cost effective control strategies under this setting.

*Q3 How can a biological control agent that is introduced to reduce an invasive species in an agricultural system affect the risk of extinction of wild plant species?*

Biological agents such as insect herbivores (e.g. weevils) can help reducing the invasive species in agricultural systems. These agents, however, can disperse to other parts of the ecosystem and target desirable species. This thesis investigates the conditions under which such dispersal can threaten biodiversity by targeting wild desirable species.

*Q4 What is the best option from an economic point of view to protect a wild plant species if it suffers from attack by a herbivore which disperses from and to the agricultural land?*

If a biological agent has spilled over from agriculture to the rest of the ecosystem and if it produces negative externalities it may be necessary to control it. The fourth research question focuses on the optimal control of the biological control agents introduced. For that reason, the ecological interactions will be modelled that determine the risk of extinction of a wild plant as a result of herbivory.

## **1.4 Methodology**

Different models have been developed in order to answer the research questions. To answer the first research question, I study cost-effective IWM strategies to control Californian thistle in New Zealand pastures in a deterministic setting. This will help to understand which combination of control options maximises net present value (NPV), how excluding risky control options (e.g. chemicals) can affect NPV and whether it is worthwhile to introduce a biological control agent (*Apion onopordi*). There are number of studies that use a dynamic optimisation approach. White and Wadsworth (1994), for instance, used a dynamic optimisation approach to find the optimal management practices for livestock grazers and harvesting grouse. Their approach maximises the net return obtained from the pasture. The same approach has been used for management of plant invasion by Kennedy (1987); Higgins et al. (1997); Wu (2001) and Odom et al. (2003) and Jones et al. (2006); and for finding optimal harvesting regimes by Bulte and van Kooten (1999). I build a novel deterministic dynamic programming model which includes 62 decision variables in two categories to control for the weed (i.e. Californian thistle). One category of decision variables includes an insect as biological control (*Apion onopordi*). This category has an irreversible effect. Once it is introduced, it will remain active in subsequent years. The other category of decision variables can be introduced annually. For the dynamics of the thistle, the model proposed by Bacher and Friedli (2002) is used. The reward function of the optimisation problem consists of benefits obtained from the pasture minus the costs of control. Annual benefits are a function of plant and animal production that depend on the area of the pasture and the thistle density. The costs of control are a sum of the costs of the control options included. The applied dynamic programming model determines the sequence of control strategies that maximises the present value of a stream of annual net benefits.



To answer the second research question, the stochastic effects of biological control agents on the target plants are studied. There have been some studies using stochastic dynamic programming looking at few control strategies, like Pandey and Medd (1991), Bulte and van Kooten (1999), and Cacho et al. (2008). The stochastic analysis in this thesis makes new contributions to the previous studies in three aspects. Firstly, I conduct a stochastic optimal control model with a discrete decision variable (consisting of 62 possible strategies) which deals with the stochasticity of introducing two biological agents: weevil (*Apion onopordi*) and mycoherbicide (*Sclerotinia sclerotiorum*). In the above mentioned studies either only a single decision variable or a few decision variable were analysed. Secondly, in this paper I look at two categories of the decision variables in a stochastic setting. One category can be chosen on an annual basis. The second category includes the introduction of the insect and has the characteristic that once the insect has been introduced it will remain active in the pasture and therefore does not have to be chosen in the later stages (irreversible). Thirdly, I focus on the stochastic efficacy of the biological control agent on the invasive plant, while the above mentioned studies mainly focused on the negative effects of biological control and less attention was paid to the success of biological control management of invasive species. The reward function, the specification of the thistle dynamics and the list of IWM strategies in the stochastic case are similar to the dynamic case. The stochastic model assumes a number of states of nature, each with a known probability of occurrence and resulting in a different efficacy of the biological control methods. The stochastic dynamic programming model determines the sequence of control strategies that maximises the expected NPV.

To answer the third research question, a biological agent that is introduced to a managed system but disperses to a natural system is studied. Currently, the conditions under which the dispersal of a biological control agent from a managed to a natural system results in a spillover effect threatening biodiversity are not systematically analysed and more work is needed to enable comprehensive assessments of risk (Rand et al. 2006). I use a novel modelling approach to find conditions under which introduction of a herbivore for biological control of a weed in agriculture, can cause extinction of a wild species in the natural compartment. A two compartment ecosystem is built: a managed (agricultural) compartment where locally a herbivore is introduced to control a pest weed and a natural compartment where the same herbivore species can attack a wild plant species. The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment herbivores attack a non-target host plant species which competes with another plant species or group of species. The main processes in the model are herbivory, competition and dispersal. The possible equilibria resulting from interaction of species are driven, and stable equilibria are found. Moreover, a sensitivity analysis is performed to identify the system characteristics that enhance or

mitigate risk, and to provide insight in the interrelationships between the different dynamic processes involved.

In order to answer the fourth research question, a bioeconomic model is developed to assess the cost effectiveness of strategies to control externalities caused by a biological agent spilled over from a managed compartment to a natural compartment. Previous studies mainly focused on the problem of invasion in agricultural or natural systems separately (e.g. Onstad et al. 2002, Crowder 2005, Dasgupta et al. 2006). The bioeconomic model uses a novel approach of a two compartment model and systematically analyses optimal control, competition, herbivory and dispersal. Benefits obtained from the managed compartment depend on the densities of endemic plants and weed in the managed compartment. Benefits obtained from the natural compartment depend on the density of the endemic wild plant species and their competitor(s). For this part, a Cobb-Douglas utility function is used. The optimal level of herbivores control is determined, that maximises net benefits obtained from the managed and the natural compartments.

This thesis makes new contributions to the literature on invasive species control in the following ways:

- Building a deterministic and stochastic dynamic programming model suitable to analyse a large number of decision variables in two categories (reversible and irreversible).
- A focus on the stochastic efficacy of biological control on invasive plants rather than on non-target plants.
- Building a two compartment ecological model accounting for herbivory, dispersal and competition.
- Building a two compartment bioeconomic model accounting for control, herbivory, dispersal and competition.

## **1.5 The structure of the thesis.**

This thesis consists of 6 chapters including the introductory chapter. Chapter 2, 3, 4 and 5 answer the research questions sequentially. Chapter 2 answers the first research question. It analyses the integrated weed management strategies which are feasible combinations of 7 control options (i.e. MCPA, MCPB, mycoherbicides, intensified grazing, introduction of insect, mowing in January, and mowing in March). A deterministic dynamic programming approach is applied to study the most cost effective ways of controlling the thistle.

Chapter 3 answers the second research question and elaborates on Chapter 2 by taking into account the stochastic effects of biological control agents (i.e. mycoherbicides and the insect) on the thistle. This chapter develops a stochastic dynamic optimisation model and analyses the most cost effective control options under such a setting.

Chapter 4 answers the third research question. This chapter focuses on a biological agent that has been introduced to a managed compartment and that spills over to a natural compartment. It analyses the conditions under which such a spillover of herbivores can cause biodiversity loss in a natural habitat. Herbivory, competition and dispersal are the main processes that are analysed.

Chapter 5 looks at the same modelling framework as Chapter 4. In this chapter, I perform an economic analysis to study the optimal control level for a herbivore which has been spilled over to a natural compartment from a managed compartment. This chapter analyses the relationship between optimal control, herbivory, competition and dispersal.

Chapter 6 summarizes the results and discusses the most important findings of the Chapters 2-5. It also provides suggestions for future studies.



## Management strategies for an invasive weed: a dynamic programming approach for Californian thistle in New Zealand

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## ABSTRACT

Invasive plants can cause significant problems in natural and agricultural ecosystems. Although research has already been conducted on the economics of a single-control option for some invasive weeds, we extended the analysis by developing a dynamic optimisation model that evaluates the net benefits of a range of possible control options simultaneously in order to identify the optimal strategy (mix of control options). This paper focuses on Californian thistle (*Cirsium arvense*) in pasture in New Zealand. The net benefit is maximised by considering the costs and efficacy of control options, and the monetary value of animal production. Trajectories of shoot density are developed and the optimal strategies are found. Our results suggest that the introduction of a biological control agent (*Apion onopordi*), in combination with one or more control options, is the optimal strategy when the initial density of the thistle population exceeds 1.0 shoot per m<sup>2</sup>. Results show that in the setting of the model excluding MCPA, MCPB and a *Sclerotinia sclerotiorum*-based mycoherbicide reduces the NPV by less than 2%.

## Keywords

Invasive plant, Pasture, Economics, New Zealand, IWM strategy, Dynamic optimisation.

## 2.1 Introduction

Weeds cause problems throughout the world in ecosystems such as pastures, natural and plantation forests, crops, golf courses, parks and reserves and natural and constructed waterways. The problems that they cause include reduced plant and animal yield, less efficient land use, higher costs of pest and plant disease control, inefficient water management, reduced natural biodiversity and lower human labour efficiency (Tyser and Key 1988; Lacey and Fay 1989; Monaco et al. 2001). Management of these problems usually requires some form of weed control, and for any particular species several possible options usually exist that may vary in both cost and effectiveness.

The cost of control options is important in assessing the feasibility of weed management. For example, replacement of perennial grass species by weeds largely reduces the productivity and contributes to a range of external costs (Vere et al. 1993; Jones and Dowling 2005). Similarly, the cost of controlling invasive weeds in pasture by the herbicide MCPA, and by a *Sclerotinia sclerotiorum*-based mycoherbicide (a fungus applied to inundate the pasture (Bourdôt and Lamoureaux 2002)) is estimated to be around US\$86 per hectare in New Zealand (Burt 2004). Other studies also highlight the excessive costs of controlling weeds (Kvist and Hakansson 1985; Harris 2002), but as the cost of damage to weeds is so high, their control is often seen as imperative. Farmers obviously need to balance the cost of control strategies against their effectiveness and long-term benefits.

In some studies the economic feasibility of controlling weeds has been assessed using net present value (NPV) and benefit-cost ratio investment criteria (Nielsen and Cronin 1977; Vere and Campbell 1984; Headley 1985; CRC 2001; McConnachie et al. 2003).

To find the optimal integrated weed management (IWM) strategy, given the dynamic character of their populations, a dynamic analysis is required that maximises net present value (NPV) of the agricultural activities. Changes in weed density according to the population dynamics of the species may be considered by applying a dynamic optimisation method that can demonstrate the effect of control. White and Wadsworth (1994) used a dynamic optimisation approach to find the optimal management practice for livestock grazers and harvesting grouse in a pasture. Their approach maximised the net return obtained from the pasture. The same approach has been used by Taylor and Burt (1984); Kennedy (1987); Higgins et al. (1997); Bulte and van Kooten (1999); Wu (2001) and Odom et al. (2003).

Californian thistle (*Cirsium arvense*) is found in both perennial and annual crops in Eurasia and America, as well as New Zealand, and it is considered one of the “world’s worst weeds” (Friedli and Bacher 2001). Californian thistle is a big problem as it restricts the area available for grazing livestock and reduces the plant yield (Donald 1990). O’Sullivan et al. (1982, 1985) showed that 20 Californian thistle shoot/m<sup>2</sup> significantly reduced crop yields by 26 to 51%.

New Zealand is a country with a very diverse and valuable natural resource base which is widely invaded by Californian thistle (Bourdôt et al. 1995). It affects pastures and arable land throughout both main islands (Bascand and Jowett 1982; Bourdôt and Kelly 1986). Californian thistle has a high growth rate and can occupy the pastures very rapidly (G W Bourdôt and D Leatwick unpublished data). This renders the pasture unusable in a short period of time. Control of the thistle by herbicides and mowing costs NZ\$27 million per annum, including costs of vaccination for scabby mouth disease in sheep in the heavily infested Southland and Otago regions in New Zealand. This cost is promoted by wounds around the mouths of grazing animals caused by the thistle's spines (Gourlay 2004). The total annual cost of the Californian thistle to New Zealand pastures, through both the cost of control and losses related to pasture production, has not been estimated but will greatly exceed this value (Bourdôt et al. 2005).

In this study we combine knowledge of ecology (Donald 1994; Bascand and Jowett 1982; Bourdôt and Kelly 1986; Bourdôt et al. 2005) and relevant economics in a bio-economic framework. An integrated weed management (IWM) approach that emphasises the use of several control measures is suggested to be the most effective way of controlling invasive plants (Miller et al. 1992; Buckley et al. 2004). Our objective is to study cost-effective IWM strategies to control Californian thistle in New Zealand pastures.

The IWM strategy is likely to differ depending on the conditions of the site, specifically the initial density and growth potential of the thistle population. We use a similar method of maximising NPV to that which was used by White and Wadsworth (1994) and Odom et al. (2003), but have extended the analysis by including two categories of strategies. The first category concerns IWM strategies that can be selected annually such as mowing or the use of herbicides. The second category includes a once-and-for-all choice to introduce an insect as a bio-control agent, in this case the weevil *Apion onopordi*, which is expected to reduce the population growth rate of Californian thistle if it were to be released in New Zealand (currently under consideration). Once the insect has been introduced it is assumed that it will remain active. It will take time to become established throughout the country, but after that, its effects on thistle dynamics can be expected to continue into the future. The optimal IWM decisions are therefore analysed under three scenarios. Firstly, the insect is not considered as a control option. Secondly, the insect is considered as an option. Thirdly, the optimal IWM decision is found for a setting in which the insect has already been introduced and is widely established. In each scenario, two groups of control options are considered. In the first group *all* possible control options are included, and in the second group, control options are excluded that might become unavailable in the future due to their perceived negative environmental impacts (e.g. herbicides) or lack of commercial viability (e.g. mycoherbicides). For each of those groups the NPV's are compared. This choice of scenarios, especially the distinction between the annual and the once-and-for-all strategies, has consequences for the



formulation of the model. Different from other comparable models, we introduce a binary variable in identifying the optimal strategy that complicates solving the model.

We first present a materials and methods section that includes the model of pasture output, the dynamics of Californian thistle and IWM strategies. Next, we describe the optimisation model. Finally, we present the results and draw conclusions.

## 2.2 Material and methods

Weeds can reduce pasture plant and animal production (Buchanan 2000; Monaco et al. 2001). Lower grazing capacity translates into lower animal production per unit area of pasture (Barrons 1969; Morrison 1972). To increase the output of pasture, control treatments are used to reduce weed density and spread. In this study, various combinations of possible control treatments for Californian thistle are considered. An optimisation model is parameterised to find the best management policy based on maximising the net benefit obtained from the pasture. The optimisation model on one hand allows for analysis of all possible IWM strategies available and on the other hand it captures the dynamic interaction between IWM systems and weed density.

Californian thistle, one of the most troublesome weeds, causes large reductions in pasture production (Holm et al. 1977; Friedli and Bacher 2001). It has invaded large areas of New Zealand. This study focuses on sheep pastures in Canterbury, one of the main provinces invaded by Californian thistle. It initially colonises pastures by seed, but subsequently it is the root system that plays the main role in population maintenance and spread. The propagative roots can penetrate 2 m into the soil (Nadeau 1988), thereby escaping the disturbance caused by tillage (Donald 1994) and harsh environmental conditions (Nadeau and Vanden 1990).

### 2.2.1 The model of pasture output

The net annual benefit obtained from pasture ( $B$ ) in year  $t$ , (NZ\$/ha), is presented in the following function:

$$B_t = BP_t - C_t \quad (1.1)$$

where,  $BP_t$  are benefits obtained from the pasture and  $C_t$  are the costs of controlling Californian thistle at time  $t$  (NZ\$/ha).

Benefits obtained from pasture ( $BP_t$ ) are defined by:

$$BP_t = P \times SU_t \quad (1.2)$$

where,  $P$  is the monetary value of one unit of livestock product in terms of gross margin, and  $SU_t$  is the number of stock units carried per ha in year  $t$ .

Stock unit production is specified as:

$$SU_t = \frac{1}{\kappa} \times Y_t \quad (1.3)$$

where,  $\kappa$  is kilograms (kg) forage production used by one livestock unit per year, and  $Y_t$  is forage production ( $\text{kg ha}^{-1} \text{ year}^{-1}$ ).  $k$  is considered to be 550 kg (Rattray 1986). The value of  $k$  depends on the conditions of the site and can deviate from our estimate because much of the forage in a pasture is not utilised by livestock, especially in the presence of the thistle. More research is needed to obtain a more precise estimate of  $k$ . In order to analyse the sensitivity of results to deviations of  $k$  a sensitivity analysis is presented in the results section. Forage production per year is defined by a model that describes crop yield loss as a function of weed density (Cousens 1985) in the following equation:

$$Y_t = \gamma \times (1 - \zeta \times D_t / (100 \times [1 + (\zeta \times D_t / \alpha)])) \quad (1.4)$$

where,  $\gamma$  is the annual yield of dry matter ( $\text{kg/m}^2$ ) in the absence of weed,  $\zeta$  is percentage of yield loss per Californian thistle shoot as the density of shoots approaches zero and  $\alpha$  is percentage loss in yield as the density of the Californian thistle shoots approaches infinity. The values of  $\gamma$ ,  $\zeta$  and  $\alpha$  for pasture lands in Canterbury, New Zealand, are set at 8.5, 5, and 100 respectively, based on research and knowledge of AgResearch centre staff who are specialists on the ecology of Californian thistle in New Zealand (G W Bourdôt and D Leathwick unpublished data).

### 2.2.2 Dynamics of Californian thistle

The dynamics of Californian thistles are defined using the model of Bacher and Friedli (2002):

$$D_{t+1} = r \times D_t \times (1 - (D_t / \mu)) + D_t \quad (1.5)$$

This model is a standard logistic growth function that is used in many biological models to measure changes in populations, where  $D_t$  is the state variable which represents the density of Californian thistle shoots in year  $t$ . Control measures taken in year  $t$  affect the density of the shoot population in the following year,  $t+1$ . Parameter  $\mu$  is the carrying capacity of shoots per square meter of land. Its value is constant and is not affected by control treatments. The value of  $\mu$  is set at 80 shoot/ $\text{m}^2$  (Bourdôt et al. 1995; Hurrell et al. 2001). The parameter  $r$  is the maximum rate of increase in shoot density. It is influenced by the ecological conditions of a site. The value of  $r$  is set at a best estimate of 2.5. Note that there are many environmental factors such as natural disease level, aphid attack, plant competition and drought that influence the value of  $r$ . These factors may vary from year to year. There were no data available that show variability of the growth rate, therefore we used the estimated value for  $r$ . Sensitivity analysis shows that an 8 percent change in the value of  $r$  does not change the optimal strategy adopted.

Introduction of the bio-control agent *Apion onopordi*, a weevil, is assumed to reduce the value of  $r$  by a constant over time. Other control treatments do not change  $r$ . Fig. 2.1 shows the phase diagram of Californian thistle shoot density over time in the absence of any control

treatment according to Equation (5). Note that due to the high growth rate it is possible that for a short period of time density exceeds carrying capacity. If this happens, net growth will fall in the year after and the density will reduce to the carrying capacity or a lower level.

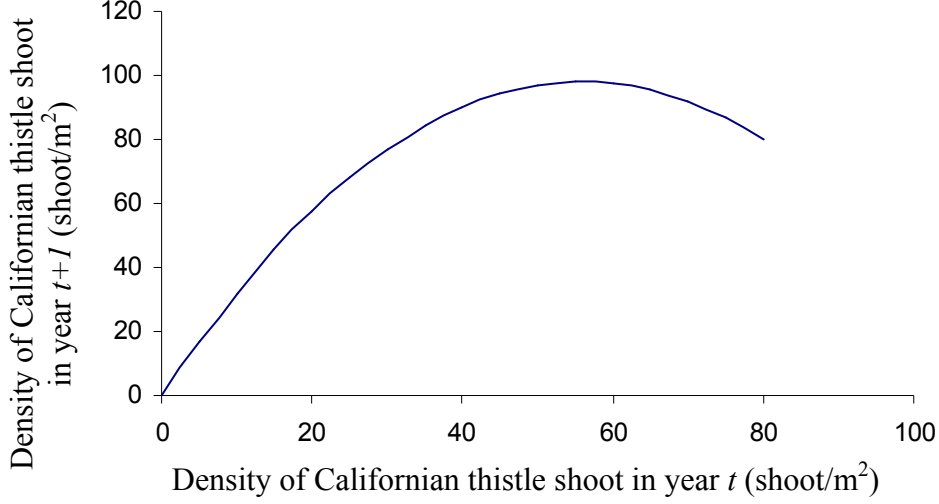


Fig. 2.1: The dynamics of Californian thistle. The density of the thistle shoot in year  $(t+1)$  is given as a function of shoot density in year  $t$  as described by Equation (5) without control.

The impacts of various IWM strategies and their costs are shown in Table 2.1.  $N$  and  $L$  are multiplier vectors for density ( $D_t$ ) and shoot population growth rate ( $r$ ) respectively defining the efficacy of the control options (Table 2.1). For instance, for strategy 1, where none of the control options are chosen, the values of  $N$  and  $L$  are 1.0, which means they have no effect on the dynamics of the Californian thistle shoot population. By comparison, strategy 11, which has values 0.7 for  $L$  and 0.18 for  $N$ , reduces the value of  $r$  by 30% and reduces  $D_t$  by 82%. Some of the parameter values for efficacies of the IWM strategies on the thistle were obtained from published studies but if no published data were available, best estimates were made based on expert knowledge about weed management in New Zealand.

### 2.2.3 IWM strategies

We consider seven options for controlling the Californian thistle in New Zealand:

*Applying MCPA.* MCPA ((4-chloro-2-methylphenoxy) acetic acid) is a systemic herbicide that gives temporary control but severely damages nitrogen-fixing clovers in treated pasture.

Table 2.1. IWM strategies, their efficacy and costs. The values of N (multiplier for the thistle density) and L (multiplier for the thistle growth) were calculated from published data when available (see “Source” column), or were estimated by GWB<sup>1</sup> and DL<sup>2</sup> when published data was not available. Costs were obtained from Burt (2003). Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), In.Gr. (intensified grazing), Ins (*Apion onopordi*).

IWM Strateg y	Control decisions							Efficacy		Cost (\$NZ/ha)	Source
	1 MC PA	2 MC PB	3 My c.	4 Mo. M.	5 Mo. J.	6 In. Gr.	7 Ins.	N	L		
1	0	0	0	0	0	0	0	1.00	1	0	
2	1	0	0	0	0	0	0	0.26	1	90.8	Hartley <i>et al.</i> (1984)
3	0	1	0	0	0	0	0	0.28	1	98	Hartley <i>et al.</i> (1984)
4	0	0	1	0	0	0	0	0.40	1	115	Hurrell <i>et al.</i> (2001)
5	0	0	0	1	0	0	0	0.57	1	75	Bourdôt <i>et al.</i> (1998)
6	0	0	0	0	1	0	0	0.50	1	75	Bourdôt <i>et al.</i> (1998)
7	0	0	0	0	0	1	0	0.29	1	34	Hartley <i>et al.</i> (1984)
8	0	0	0	0	0	0	1	0.68	0.7	3	Friedli and Bacher (2001)
9	1	0	0	0	1	0	0	0.13	1	165.8	GWB and DL
10	1	0	0	0	0	1	0	0.08	1	124.8	GWB and DL
11	1	0	0	0	0	0	1	0.18	0.7	93.8	GWB and DL
12	1	0	0	0	1	1	0	0.04	1	199.8	GWB and DL
13	1	0	0	0	1	0	1	0.09	0.7	168.8	GWB and DL
14	1	0	0	0	0	1	1	0.05	0.7	127.8	GWB and DL
15	1	0	0	0	1	1	1	0.03	0.7	202.8	GWB and DL
16	0	1	0	0	1	0	0	0.14	1	173	GWB and DL
17	0	1	0	0	0	1	0	0.08	1	132	Hartley <i>et al.</i> (1984)
18	0	1	0	0	0	0	1	0.19	0.7	101	GWB and DL
19	0	1	0	0	1	1	0	0.04	1	207	GWB and DL
20	0	1	0	0	1	0	1	0.10	0.7	176	GWB and DL
21	0	1	0	0	0	1	1	0.06	0.7	135	GWB and DL
22	0	1	0	0	1	1	1	0.03	0.7	210	GWB and DL
23	0	0	1	0	1	0	0	0.20	1	190	GWB and DL
24	0	0	1	0	0	1	0	0.12	1	149	GWB and DL
25	0	0	1	0	0	0	1	0.27	0.7	118	GWB and DL
26	0	0	1	0	1	1	0	0.06	1	224	GWB and DL
27	0	0	1	0	1	0	1	0.14	0.7	193	GWB and DL
28	0	0	1	0	0	1	1	0.08	0.7	152	GWB and DL
29	0	0	1	0	1	1	1	0.04	0.7	227	GWB and DL
30	0	0	0	1	1	0	0	0.29	1	150	Bourdôt <i>et al.</i> (1998)
31	0	0	0	1	0	1	0	0.17	1	109	GWB and DL
32	0	0	0	1	0	0	1	0.39	0.7	78	GWB and DL
33	0	0	0	1	1	1	0	0.08	1	184	GWB and DL
34	0	0	0	1	1	0	1	0.20	0.7	153	GWB and DL
35	0	0	0	1	0	1	1	0.11	0.7	112	GWB and DL
36	0	0	0	1	1	1	1	0.06	0.7	187	GWB and DL
37	0	0	0	0	1	1	0	0.15	1	109	GWB and DL
38	0	0	0	0	1	0	1	0.34	0.7	78	GWB and DL
39	0	0	0	0	0	1	1	0.20	0.7	37	GWB and DL
40	0	0	0	0	1	1	1	0.10	0.7	112	GWB and DL
41	1	0	1	0	0	0	0	0.10	1	205.8	GWB and DL
42	0	1	1	0	0	0	0	0.11	1	213	GWB and DL
43	0	0	1	1	0	0	0	0.23	1	190	GWB and DL
44	1	0	1	0	1	0	0	0.05	1	280.8	GWB and DL
45	1	0	1	0	0	1	0	0.03	1	239.8	GWB and DL

<sup>1</sup> Bourdôt, G.W.

<sup>2</sup> Leathwick, D.

Table 2.1 (*continued*)

IWM Strateg y	Control decisions							Efficacy		Cost (\$NZ/ha)	Source
	1 MC PA	2 MC PB	3 My c.	4 Mo. M.	5 Mo. J.	6 In.G r.	7 Ins.	N	L		
46	1	0	1	0	0	0	1	0.07	0.7	208.8	GWB and DL
47	0	1	1	0	1	0	0	0.06	1	288	GWB and DL
48	0	1	1	0	0	1	0	0.03	1	247	GWB and DL
49	0	1	1	0	0	0	1	0.08	0.7	216	GWB and DL
50	0	0	1	1	1	0	0	0.11	1	265	GWB and DL
51	0	0	1	1	0	1	0	0.07	1	224	GWB and DL
52	0	0	1	1	0	0	1	0.16	0.7	193	GWB and DL
53	1	0	1	0	1	1	0	0.02	1	314.8	GWB and DL
54	1	0	1	0	1	0	1	0.04	0.7	283.4	GWB and DL
55	1	0	1	0	0	1	1	0.02	0.7	242	GWB and DL
56	0	1	1	0	1	1	0	0.02	1	322	GWB and DL
57	0	1	1	0	0	1	1	0.02	0.7	250	GWB and DL
58	0	0	0	1	1	1	1	0.06	0.7	187	GWB and DL
59	0	0	1	1	1	1	0	0.03	1	299	GWB and DL
60	0	0	1	1	1	0	1	0.08	0.7	268	GWB and DL
61	0	0	1	1	0	1	1	0.01	0.7	227	GWB and DL
62	0	0	1	1	1	1	1	0.02	0.7	302	GWB and DL

This herbicide is one of the most effective ways of quickly reducing thistle shoot density, and therefore can be important in increasing the production from the pasture (Barrons 1969). In this study the benefit lost by removing clover is included in the price of the MCPA option.

*Applying MCPB.* MCPB (4-(4-chloro-2-methylphenoxy) butanoic acid) is closely related to MCPA. MCPB does not damage clover. This is considered to be its advantage over MCPA. MCPB, however, is more expensive than MCPA.

*Applying mycoherbicides.* These are plant pathogens that can control weeds in a similar way to herbicides (Trujillo and Templeton 1981; Charudattan 1991). While the fungus *Sclerotinia sclerotiorum* is under development as a mycoherbicide for weed control in New Zealand pastures, uncertainty remains regarding its eventual commercialisation.

*Mowing in January.* Mowing is a mechanical option for controlling Californian thistle. In this method the arms and knives of machines remove the thistle's foliage, which results in reduced root growth and reduced shoot production (Bourdôt et al. 1998).

*Mowing in March.* The same technique used as above, however mowing now occurs in March.

*Intensified grazing.* Grazing animals such as goats, sheep, and cattle at sufficiently high intensity can control invasive species in rangelands. The grazing of weeds damages their physiology, controls their spread (Mitchell and Abernethy 1993) and has proven effect against Californian thistle (Hartley et al. 1984).

*Biological control.* Insect herbivores can be used to control weeds. They usually come from the native habitat of the weed; their interactions with plants are complex and must be extensively tested to ensure that they will not attack plants other than those being targeted

(Bernays and Chapman 1994). Such insects, once established, can often support their own growth and expansion. Here we consider the weevil, *Apion onopordi*, a putative biological control agent for Californian thistle being considered for release in New Zealand.

There are other ways of controlling weed that have not been considered in our model. For example the selective use of trans-located herbicides, such as glyphosate, by wiping equipment or re-grassing a paddock, with glyphosate using the method of boom-spraying. Farmers do not normally choose these methods because of their damage to the vegetation and because the pasture renewal rate in New Zealand is very low (Clark et al. 2007). However, in a more extensive study these options might also be included in the analysis.

To determine the efficacy of combining several control options, a full matrix of all possible combinations of these seven control options was constructed (Table 2.1). The rows of this matrix represent the IWM strategies and the columns are the control options. The values in this matrix were set to 0 (indicating that the corresponding option is not included in the strategy) or 1 (meaning that the particular control option is included). For instance, strategy 1 is a 'do nothing' or 'no control' strategy in which all values of the row are zero. For strategy 16, control options numbers 2 and 5 were set to 1, while the others were set to zero, indicating that this strategy is a combination of MCPB and mowing in January. All possible combinations of control options yield a total of 128 potential strategies. However, some strategies are illogical and are therefore excluded, e.g. the two herbicides (MPCA, and MPCB) and mowing in January have the same time of application. Excluding all the illogical strategies results in a final matrix of 62 strategies (Table 2.1).

To determine the values of the IWM strategy efficacy vectors  $N$  and  $L$ , each individual control option was itself first allocated an efficacy, based on published data (see Table 2.1). For combinations of control options (strategies), the efficacies were taken from published data where available. In the absence of empirical data the IWM strategy efficacy vector values were calculated assuming that the actions of the component options were independent and multiplicative. It is, however, possible that the combination of control options have synergetic effects on the thistle different from that which has been presented in Table 2.1. We have not been able to trace the information in literature, which suggests that further detailed research is required to obtain more reliable efficacies when different control options are combined. A sensitivity analysis will be presented in the results section to show the effect of alternative efficacies on the optimal IWM strategy chosen. Thus for strategy 9 (MCPA + mowing in January) the proportion of thistle shoots surviving both treatments was  $N = 0.26 \times 0.5 = 0.13$  (Table 2.1).

### 2.2.4 Optimisation model

The objective of the deterministic model is to choose a sequence of control strategies,  $u_t$ , that maximises the present value of a stream of annual net benefits,  $V_t$ . Decision variable ( $u_t$ ) is a discrete variable and corresponds to the IWM strategy adopted in year  $t$ . The number of control strategies that a decision maker can choose from is given by  $ns$ , where  $1 \leq u_t \leq ns$ . Note that the set of control strategies  $cs = \{1, \dots, ns\}$  can be subdivided into two subsets:  $cs_{NI} = \{1, \dots, ns_{NI}\}$  and  $cs_I = \{ns_{NI} + 1, \dots, ns\}$ , with  $cs_{NI}$  the set of strategies that do not include the introduction of the insect, and  $cs_I$  the set of strategies that do include the introduction of the insect.  $ns_{NI}$  represents the number of strategies that do not include the introduction of the insect. Once one of the strategies from set  $cs_I$  has been adopted, the decision maker can only choose from set  $cs_{NI}$  in the subsequent years.

The optimisation problem for year  $t$  is given in the following equation:

$$V_t(D_{t-1}) = \max_{u_t} [B_t(D_t, u_t) + \delta V_{t+1}(D_t)] \quad (1.6)$$

Subject to:

$$D_t = (r \times L(u_t)) \times (D_{t-1} \times N(u_t) \times (1 - (D_t \times N(u_t)) / \mu)) + (D_t \times N(u_t)) \quad (1.7)$$

where  $D_t$  represents the density of the thistle at the end of year  $t$  and  $\delta$  represents the discount factor. In equation (1.6) the future net benefit,  $V_{t+1}$ , is affected by the density of the thistle shoots at the end of year  $t$ ,  $D_t$ . The net benefits in year  $t$  are affected by the IWM strategy adopted in year  $t$ ,  $u_t$  and the shoot density resulting from applying this strategy. The Dynamic Programming model was solved for a planning time horizon of 40 years using GAMS (General Algebraic Modeling System) (Brooke et al. 1992).

All costs and prices are expressed in New Zealand dollars. Prices for sheep production are in terms of gross margin and are obtained from Burt (2004).

The costs of the herbicide control options were calculated by adding spraying costs to the price of the herbicide. MCPB (and a mycoherbicide based on *Sclerotinia sclerotiorum*) are more selective than MCPA in controlling Californian thistle without damaging clovers. The damage to clovers resulting from the application of MCPA is equivalent to a 2% loss in gross margin (Popay et al. 1989), and was added to the cost of MCPA.

Grazing is one method to control the thistle (Hartley et al. 1984). Californian thistle is not a palatable plant and animals do not choose it unless there is no other food available. In order to force animals to graze on the thistle, intensified grazing should be applied. Intensified grazing makes animals less selective and reduces the quality of their diet, resulting in reduced weight gain. The average stock unit for sheep pastures in the Canterbury province is 12 stock unit per hectare (P Kemp unpublished data). In order to control the thistle we will

increase the number of sheep stock unit to 20 per hectare for one month at the early growth stage of the thistle shoots. Intensified grazing as such would cause a weight loss of 1.5 kg per stock unit (P Kemp unpublished data). 1.5 kg loss per stock unit would result in 30 kg loss per hectare for 20 stock units per hectare. This is equivalent to 0.5 stock units per hectare. The cost of grazing was therefore calculated by multiplying 0.5 by the price of a sheep stock unit (in terms of gross margin). The cost of introduction and establishment of the insect *Apion onopordi* in New Zealand is estimated to be around NZ\$500,000. Dividing this cost by the area of invaded pastures by Californian thistle, gives the cost of the insect introduction per unit of land.

## 2.3 Scenarios and results

The impact of the insect, *Apion onopordi*, on thistle shoot population dynamics is different from that of the other control options. Not only is the insect applied nationally, once it has been introduced and has established, its impact on the thistle is expected to be permanent. We therefore analyse three main scenarios. For Scenario “no insect”, *Apion onopordi* has not been introduced and the insect is not available to be released. Therefore the insect is not included in the control options. For Scenario “insect available”, *Apion onopordi* has not been introduced but is available to be released into pastures. Therefore the insect is included in the control options. For Scenario “insect released”, *Apion onopordi* has been released and is actively present and therefore not included in the control options. In addition, some control options such as MCPA, MCPB and mycoherbicides can be considered damaging to the environment (e.g. by “green consumers”), and some farmers may prefer not to apply them. Although these herbicides could be more cost efficient and beneficial from an economic point of view, we also want to evaluate the effect on the net benefit of excluding these herbicides. Therefore each of the three scenarios was divided into two sub-scenarios. In the first sub-scenario, herbicides are included in the controlling options and in the second, herbicides are excluded. The NPV's of these two sub-scenarios are compared and the optimal decision and optimal state transition of each sub-scenario are presented given the newly imposed conditions.

### 2.3.1 The change in Californian thistle shoot population density under optimal strategies

In Fig. 2.1 the relationship between densities of Californian thistle shoot in year  $t$  and year  $t+1$  is shown. Without control treatments the weed population increases rapidly due the value of  $r$  (Equation 5). In contrast, application of the optimal control strategies results in the maintenance of low thistle densities. Fig. 2A-B show that when herbicides are excluded, the density of the thistle in year  $t+1$  is higher than in scenarios with herbicides. The main reason for this is that by excluding the control options that are cost effective and that have a high



efficacy, like MCPA, the density of the thistle remains higher. It also shows that when the insect is not present and is thus not an option, the optimal density of Californian thistle is higher than scenarios with the insect. This difference is larger when herbicides are excluded from the model.

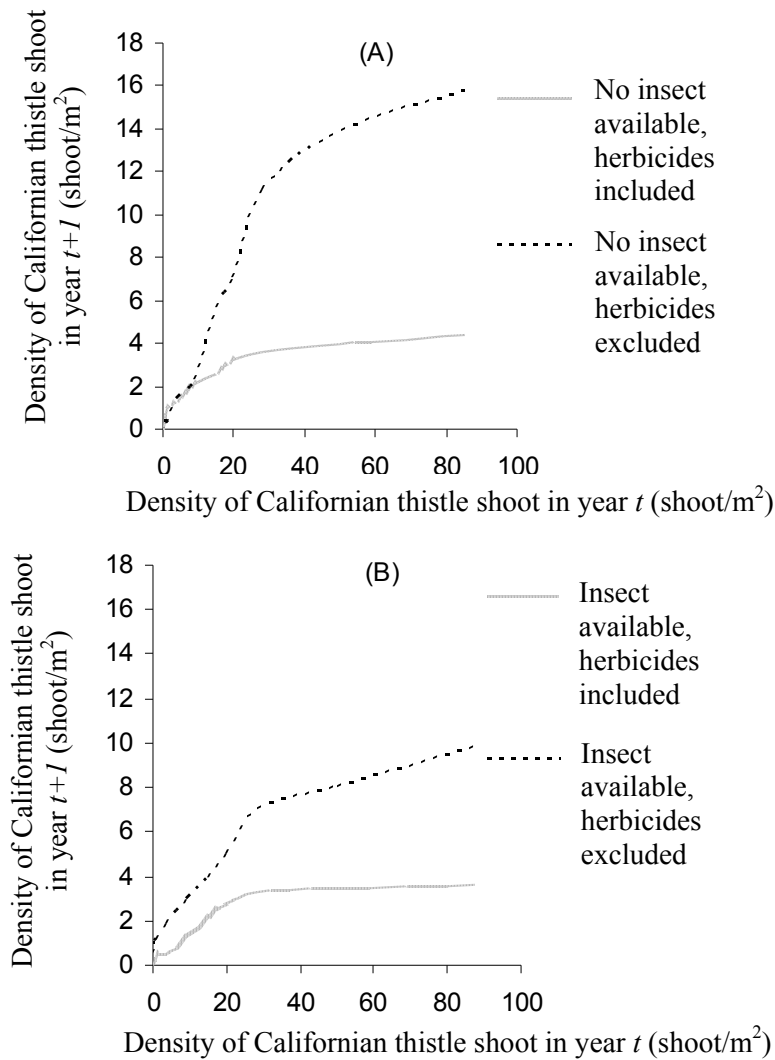


Fig. 2A-B: Changes in Californian thistle shoot population density under optimal strategies. The insect is not available for (A), and is available or already released for (B).

### 2.3.2 The optimal IWM strategies:

#### *The optimal strategies for Scenario “no insect”*

The optimal strategies when the bio-control agent *Apion onopordi* was not introduced and was not available to be released are presented for different ranges of initial weed density (see Table 2.2). Where the initial density of thistle is lower than 1 shoot per  $m^2$  the optimal IWM strategy is number 7, i.e. intensified grazing. For pastures where the initial density is between

1 and 15 shoot per m<sup>2</sup> the optimal IWM strategy for when herbicides are included is number 10, i.e. MCPA and intensified grazing, and when herbicides are excluded the optimal strategy is number 33, i.e. mowing in March, mowing in January and intensified grazing. For areas where the initial density is between 15 and 40 shoot per m<sup>2</sup> and when herbicides are included the optimal strategy, the number is 12, i.e. MCPA, mowing in January and intensified grazing, and when herbicides are excluded the number is 33, i.e. mowing in March, mowing in January and intensified grazing. For pastures where the initial density is more than 40 shoot per m<sup>2</sup> and when herbicides are available the optimal IWM strategy is number 53, i.e. MCPA, mycoherbicides, mowing in January and intensified grazing, and when herbicides are excluded the optimal IWM strategy is number 33, i.e. mowing in March, mowing in January and intensified grazing.

Table 2.2: Optimal starting strategies for different ranges of initial thistle. The insect is either not available, available or has been released. Herbicides are either included or excluded\*

Initial Californian thistle density (shoot/m <sup>2</sup> )	With herbicides		Without herbicides	
	No insect		No insect	
	IWM strategy	Control decisions	IWM strategy	Control decisions
0.00-1	7	In. Gr.	7	In. Gr.
1-15	10	MCPA, In. Gr.	33	Mo.M., Mo.J., In. Gr.
15-40	12	MCPA, Mo.J., In. Gr.	33	Mo.M., Mo.J., In. Gr.
40-100	53	MCPA, Myc., Mo.J., In. Gr	33	Mo.M., Mo.J., In. Gr.
	Insect available		Insect available	
	IWM strategy	Control decisions	IWM strategy	Control decisions
0.00-1	7	In. Gr.	7	In. Gr.
1-3	39	In. Gr., Ins.	39	In. Gr., Ins.
3-7	14	MCPA, In. Gr., Ins.	40	Mo.J., In. Gr., Ins.
7-27	14	MCPA, In. Gr., Ins.	58	Mo.M., Mo.J., In. Gr., Ins.
27-79	15	MCPA, Mo.J., In. Gr., Ins	58	Mo.M., Mo.J., In. Gr., Ins.
79-100	55	MCPA, Myc., In. Gr., Ins.	58	Mo.M., Mo.J., In. Gr., Ins.
	Insect released		Insect released	
	IWM strategy	Control decisions	IWM strategy	Control decisions
0-1	7	In. Gr.	7	In. Gr.
1-7	10	MCPA, In. Gr.	37	Mo.J., In. Gr.
7-19	10	MCPA, In. Gr.	33	Mo.M., Mo.J., In. Gr.
19-51	12	MCPA, Mo.J., In. Gr.	33	Mo.M., Mo.J., In. Gr.
51-100	53	MCPA, Myc., Mo.J., In. Gr	33	Mo.M., Mo.J., In. Gr.

\*Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), In.Gr. (intensified grazing), Ins. (*Apion onopordi*).

### *The optimal strategies for Scenarios " insect available "*

The optimal strategies for different ranges of thistle density, when the bio-control agent *Apion onopordi* is an option, are presented in Table 2.2.

Herbicides are either included or excluded. Where the initial density of thistle is lower than 1 shoot per m<sup>2</sup> the optimal IWM strategy is number 7, i.e. intensified grazing. If the initial density is between 1 and 3 shoot per m<sup>2</sup> the optimal IWM strategy is number 39, i.e.

intensified grazing and introduction of the insect. For pastures in which herbicides are included, the optimal IWM strategy is: 1) number 14, i.e. MCPA, intensified grazing and introduction of the insect if the density of the thistle is between 3 and 27 shoots per  $\text{m}^2$ , 2) number 15, i.e. MCPA, mowing in January intensified grazing and introduction of the insect if density of the thistle is between 27 and 79 shoots per  $\text{m}^2$  and 3) number 55, i.e. MCPA, mycoherbicides, intensified grazing and the insect when the density of the thistle is larger than 79 shoots per  $\text{m}^2$ . For pastures in which herbicides are excluded, the optimal IWM strategy is 1) number 40, i.e. mowing in January, intensified grazing and introduction of the insect when the density of the thistle is between 3 and 7 shoots per  $\text{m}^2$  and 2) number 58, i.e. mowing in March, mowing in January, intensified grazing and the insect when the density of the thistle is larger than 7 shoots per  $\text{m}^2$ .

#### *The optimal strategies for Scenario "insect released"*

If the insect has already been released, optimal strategies are roughly comparable with those discussed in the previous section (Scenario "insect available"), with the difference being that the insect does not have to be introduced any more. However, there are some small differences in densities at which particular options are adopted (Table 2.2). These differences are caused by differences in costs. This is because no cost has to be made to introduce the insect when the insect has already been released. Another reason for these small differences is that for Scenario "insect released" the insect has already had its influence on the thistle from the first year.

### **2.3.3 Optimal path of IWM strategies**

A useful feature of dynamic programming is that it produces a decision rule based on the state of the system at any time, as presented in the previous section. It is also possible to see which sequences of strategies are optimal after several years of applying optimal strategies. The optimal strategies for six years are shown in Table 2.3, assuming the initial density of thistle is 20 shoots per  $\text{m}^2$ . We chose this density randomly just to present an example of optimal trajectory. The results suggest that it is optimal to drive the thistle population to a low density of less than 1 shoot per  $\text{m}^2$  (which occurs by year 4) and maintain its low value by intensified grazing. The results show that when the insect is not available and herbicides are excluded it takes more time to reach an optimal low density. The reason for this is that herbicides are more effective and reduce thistle density more rapidly. The insect also helps to suppress the density of the thistle. Therefore the time that is needed to bring the thistle density to an optimal low level is shorter when the strategies include the insect (Table 2.3).

Table 2.3: Optimal decision options for year  $t$ , when the initial density of the thistle is 20 shoots/m<sup>2</sup>. The insect is either not available, available or has been released. Herbicides are either included or excluded \*

Year ( $t$ )	With herbicides			Without herbicides		
	No insect			No insect		
	Density (shoots/m <sup>2</sup> )	IWM strategy	Control decisions	Density (shoots/m <sup>2</sup> )	IWM strategy	Control decisions
1	20	12	MCPA, Mo.J., In.Gr.	20	33	Mo.M., Mo.J., In.Gr.
2	3	10	MCPA, In.Gr.	5	33	Mo.M., Mo.J., In.Gr.
3	2	10	MCPA, In.Gr.	4	33	Mo.M., Mo.J., In.Gr.
4	>1	7	In.Gr.	2	33	Mo.M., Mo.J., In.Gr.
5	>1	7	In.Gr.	>1	7	In.Gr.
6	>1	7	In.Gr.	>1	7	In.Gr.
1	Insect available			Insect available		
	Density (shoot/m <sup>2</sup> )	IWM strategy	Control decisions	Density (shoot/m <sup>2</sup> )	IWM strategy	Control decisions
	20	14	MCPA, In.Gr., Ins.	20	58	Mo.M., Mo.J., In.Gr., Ins.
2	2.5	10	MCPA, In.Gr.	4.5	37	Mo.J., In.Gr.
3	>1	7	In.Gr.	>1	7	In.Gr.
4	>1	7	In.Gr.	>1	7	In.Gr.
5	>1	7	In.Gr.	>1	7	In.Gr.
6	>1	7	In.Gr.	>1	7	In.Gr.
1	Insect released			Insect released		
	Density (shoot/m <sup>2</sup> )	IWM strategy	Control decisions	Density (shoot/m <sup>2</sup> )	IWM strategy	Control decisions
	20	12	MCPA, Mo.J., In. Gr.	20	33	Mo.M., Mo.J., In.Gr.
2	2.2	10	MCPA, In. Gr.	4	37	Mo.J., In.Gr.
3	>1	7	In.Gr.	>1	7	In.Gr.
4	>1	7	In.Gr.	>1	7	In.Gr.
5	>1	7	In.Gr.	>1	7	In.Gr.
6	>1	7	In.Gr.	>1	7	In.Gr.

\*Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), In.Gr. (intensified grazing), Ins. (*Apion onopordi*).

### 2.3.4 Optimal trajectory of shoot population density

By applying optimal strategies, the trajectory of Californian thistle shoot density is altered over time. Fig. 2.3 shows the trajectory of thistle shoot density under optimal control strategies. The model was run for 40 years. After 10 years of applying optimal IWM the density of the thistle reached its equilibrium. To simplify the presentation of the results, only the optimal trajectory of density over 10 years are presented here. In this figure a low initial thistle density (5 shoot per m<sup>2</sup>) is chosen to be able to present detailed information about the optimal shoot trajectory. For the scenarios that include the insect (Scenarios “insect available” and “insect released”), thistle density drops sharply between year zero and year 10, then the density of thistles remains within the range of 0.25 and 0.05 shoot per m<sup>2</sup>. These results imply that in the absence of the insect (Scenarios “no insect”) the density of shoots drop until year 7 and then remain at a higher range (between 0.3 and 0.45). This is due to the insect reducing the growth rate of thistle throughout time. When herbicides are included in the control options, the density stays at a lower level than in the scenarios where herbicides

are excluded. This difference is higher when the insect is not available (Scenario “no insect”) as compared to Scenarios “insect available” and “insect released”.

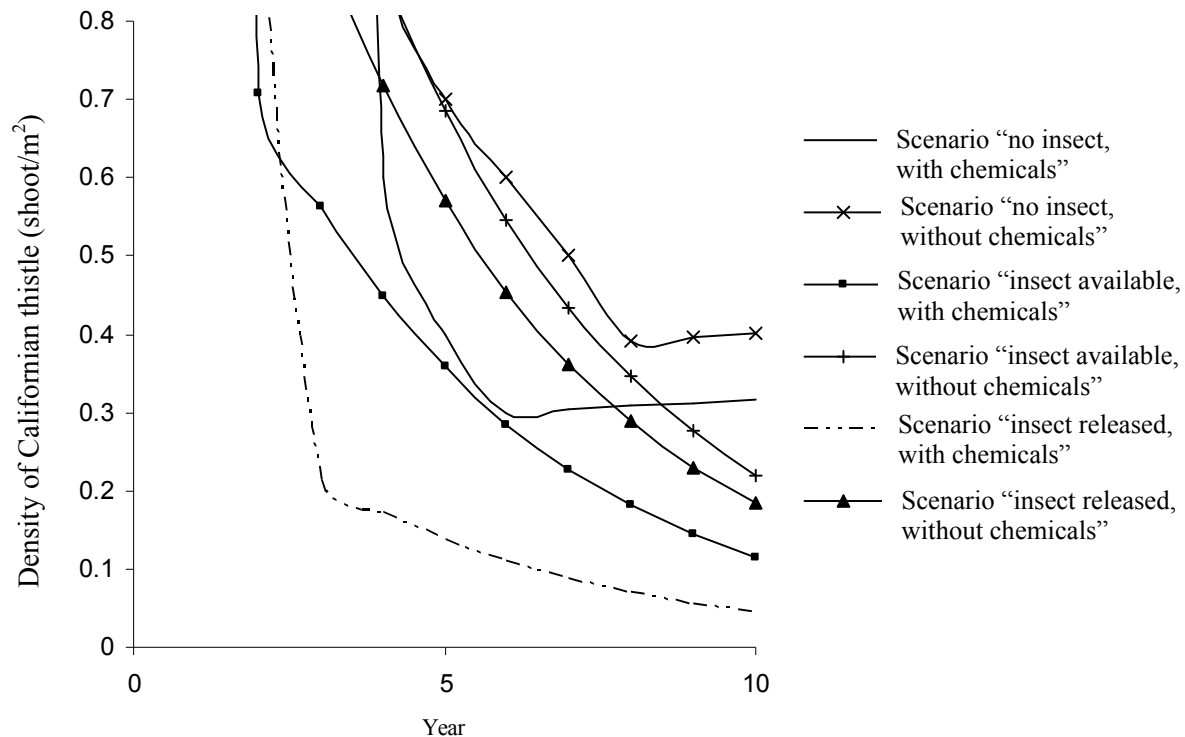


Fig. 2.3: Trajectory of the Californian thistle shoot population (shoot/m<sup>2</sup>) under any of the optimal management strategies for each of the 6 scenarios, with initial density set at 5 shoots/m<sup>2</sup>.

### 2.3.5 Net present value

Net present values (NZ\$/ha) for various initial densities of Californian thistle for a period of 40 years are presented in Table 2.4. The results show that when herbicides are excluded from control options, a slightly lower NPV is obtained. This shows that herbicides can be replaced by more environmental friendly options at a low cost. This reduction in NPV becomes slightly larger as thistle density increases. This is because under higher densities of thistle, herbicides become more cost effective.

Table 2.4: NPV (NZ\$/ha) obtained from the pasture when the insect is either not available, is available or is released. Herbicides are either included or excluded.

Initial thistle density (shoot/m <sup>2</sup> )	With herbicides	Without herbicides	Percentage decrease in NPV as herbicides are excluded
	NPV when no insect available (\$/ha)	NPV when no insect available (\$/ha)	
0.4	22548	22548	0
5	22198	22133	0.3
10	22189	22031	0.7
20	22143	21906	1.1
40	22051	21735	1.4
60	22005	21604	1.8
80	21959	21503	2.1
	NPV when the insect available (\$/ha)	NPV when the insect available (\$/ha)	
0.4	22548	22548	0
5	22471	22419	0.2
10	22423	22326	0.4
20	22348	22209	0.6
40	22269	22049	1.0
60	22215	21938	1.2
80	22184	21840	1.6
	NPV when the insect is released (\$/ha)	NPV when the insect is released (\$/ha)	
0.4	22548	22548	0
5	22516	22471	0.3
10	22450	22379	0.7
20	22387	22265	1.1
40	22312	22143	1.4
60	22262	22041	1.8
80	22213	21952	2.1

\*Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), In.Gr. (intensified grazing), Ins. (*Apion onopordi*).

The results also show that the higher the initial density of Californian thistle, the lower the NPV obtained. For all scenarios, the highest NPVs were obtained when the density of Californian thistle was 0.4. The lowest NPV occurred when the density of Californian thistle was 80 and the use of herbicides was excluded from the model. As we can see, if the insect, *Apion onopordi*, is released and herbicides are included in the model, NPV is slightly higher than under other scenarios.

It is possible to show how NPV reacts to the availability of the insect. The results show a marginally higher NPV when the insect is a control option, as compared to the scenarios where the insect is not available, if the initial density of Californian thistle is more than 1. Table 2.5 shows the difference between NPV of Scenarios “no insect” and Scenarios “insect

available” (where the insect is an option but not released) in terms of percentage. The results show that when herbicides are excluded, the absence of *Apion onopordi* results in a marginally lower NPV. This reduction in NPV becomes slightly larger as the density of Californian thistle increases. When herbicides are excluded and the density of Californian thistle is higher, the effect of the insect is more important, because the options with higher efficacy (herbicides) do not exist.

Table 2.5: The percentage decrease in net present value for different densities of Californian thistle, as a result of excluding the insect from control options.

Initial Californian thistle density	% decrease in NPV when herbicides are included	% decrease in NPV when herbicides are excluded
0.4	0	0
5	1.1	1.5
10	1.2	1.6
20	1.2	1.6
40	1.2	1.8
60	1.2	2
80	1.4	2

### 2.3.6 Sensitivity analysis

We conducted a sensitivity analysis to examine the effects of variations of parameter values on the optimal IWM strategy chosen. Table 2.6 shows for which variations in parameter values optimal strategies do not change.

The sensitivity analysis shows firstly that most of the non-economic parameters, such as  $\gamma, \alpha, \mu, g, k$  and  $\varsigma$ , that are influenced by conditions of the site, have a low impact on the strategy chosen. Secondly, efficacies of the control options have a low impact on the strategy chosen. This impact is lower when the control option is combined with other options, because when one control option is combined with other options, variation is absorbed by the other control options. For example the application of MCPA alone reduces the thistle density by 74 percent (strategy number 2) but when it is combined with mycoherbicide, mowing in March and intensified grazing (strategy number 53) the additive efficacy of MCPA is only 4.2 percent. Thirdly, variations in the economic parameters (C and particularly  $\delta$ ) have a very low effect on the strategy chosen. We conclude that within the ranges of our sensitivity analysis the model is robust against changes in the parameter values.

Table 2.6: Parameter deviations (%) and the range of their change that do not affect the optimal strategy.\*

Parameter	Deviations (%)	Range
$\gamma$	18	6.9-10
$\alpha$	50	50-100
$r$	8	2.3-2.7
$\mu$	40	48-112
$g$	20	440-660
$\zeta$	20	4-6
$S$	20	55-89
$k$	20	440-660
$\delta$	85	0.15-1.8
C	15	Depend on the strategy
N 1	10	Depend on the strategy
N 2	40	Depend on the strategy
L	14	Depend on the strategy

\*  $\gamma$  (annual yield of dry matter (kg/m<sup>2</sup>)),  $\alpha$  (percentage loss in yield as the density of the thistle shoots approaches infinity),  $r$  (growth rate of the thistle),  $\mu$  (maximum density of the thistle shoots that can grow on one square meter),  $g$  (forage production used per livestock unit per year (kg)),  $\zeta$  (Yield loss caused by the thistle as the density of shoots approaches zero(%)).  $S$  (monetary value of a livestock unit (NZ\$)),  $k$  (kg forage production used by one livestock unit per year),  $\delta$  (discount factor (1/(1+discount rate))), N 1 (density efficacy for strategies 2-8), N2 (density efficacy of a single control option within the control strategies 9-62) and L (growth rate efficacy).

## 2.4 Summary and conclusions

This paper applied a dynamic programming approach to the management of pastures that are infested with Californian thistle.

The analysis focused on the question whether the insect, *Apion onopordi*, if introduced to control Californian thistle in New Zealand, would be more beneficial alone or combined with other control options. The results show that the introduction of the insect results in a slightly higher NPV assuming that the insect has no adverse effect on other species. This implies that the insect can be excluded from the control option at a low cost, avoiding the ecological risks related to its release. It is also demonstrated that the optimal IWM strategy is to apply a combination of control options even for low densities of Californian thistle.

Regarding the lowest density that thistles will reach by applying optimal strategies in the long run and the possibility of eradication, the model shows that the density of Californian thistle decreases to 0.025 but does not reach zero. The reason for this is that all strategies reduce the density of the thistle by a certain percentage less than 100% (Table 2.1).

We showed which combinations of control options are optimal, using three scenarios and six sub-scenarios for different ranges of thistle densities. The results show that for a setting where all control options are included and the insect (*Apion onopordi*) is not available, for a



low density of thistles (density between 1 and 15), the best strategy is a combination of MCPA and intensified grazing (number 10). When the density is high (between 15 and 40) the best strategy is a combination of MCPA, mowing in January and intensified grazing (number 12). For the lower density of thistles (between 3 and 27 shoots per m<sup>2</sup>), when herbicide use is included and the insect is an option, the optimal strategy is a combination of MCPA, intensified grazing and introducing *Apion onopordi* (number 14), and for a higher percentage of Californian thistle density (density between 27 to 79) the optimal strategy is a combination of MCPA, mowing in January, intensified grazing and the insect (number 15). When the insect is actively present and herbicides are included for a lower level of Californian thistle density (density between 1 to 19 shoots per m<sup>2</sup>) the optimal strategy is a combination of MCPA, and intensified grazing (number 10). For a higher density of Californian thistle (density between 19 to 51 shoots per m<sup>2</sup>) the optimal strategy is a combination of MCPA, mowing in January and intensified grazing (number 12). The results also indicate when herbicides are excluded, the optimal strategy for a density of Californian thistle of more than 7 shoots per m<sup>2</sup> is a combination of mowing in March, mowing in January and intensified grazing (number 33).

We also analysed the influence of excluding herbicides on NPV. When they are removed from the list of control options, the NPV is reduced maximally by 2 percent therefore herbicides can be replaced by more environmentally friendly options at a cost not exceeding 2% of NPV.

The future management policy could focus on the optimal strategy to keep the density of Californian thistle at an optimal level and maximise the net present value of the pasture. For future studies we suggest more analyses on the efficacies of control strategies especially where several control options are used together and a synergic effect of combined options is possible. We also suggest to study stochastic effects of control strategies on the weed density and externalities caused by introduction of biological control agents.

## Acknowledgment

We thank Arjan Ruijs for his direction at the initial stage of developing the model. Thanks to Prof. Anton Meister for providing contacts and facilities at Massey University in New Zealand.



## Biological control of invasive plant species: a stochastic analysis

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A version of this paper in which only the stochastic effects of one control option (*Apion onopordi*) is considered has been accepted for publication in the *International Journal of Environmental Technology and Management*.

**ABSTRACT**

Invasive species are considered to be a great threat to natural ecosystems. It is recognised that biological agents have a potential to control invasions. Due to the stochastic effect of biological control however, it is possible that the biological agent does not function properly. In this paper, we analyse to what extent stochastic effects of biological control (i.e. by means of introducing the weevil *Apion onopordi* or by using mycoherbicides) affect the optimal choice of control strategies to deal with the invasive Californian thistle in New Zealand. A stochastic, dynamic optimisation model was set up to derive the path and combination of control options that maximise the expected net present value of returns from a pasture. We analysed three different situations: (i) a deterministic case without stochasticity, (ii) a case with a stochastic effect of introducing the weevil *Apion onopordi* to reduce thistle density and (iii) a case in which the effect of applying mycoherbicides to reduce thistle density is stochastic. Results show that the stochasticity of the efficacy of the weevil does not affect the optimal control measure adopted. Compared to the deterministic case however, mycoherbicides will be introduced at a higher level of weed density if we take the stochastic effect of mycoherbicides into account. On the basis of the results we argue that chemicals such as MCPA can be replaced by more environmentally friendly control options at relatively low costs.

**Keywords**

Invasive species, stochastic optimisation, economics, biological control.

### 3.1 Introduction

Alien invasive species are a significant threat to biodiversity, threatening significant percentages of listed rare and endangered native plant species (Pimental 2002b). Alien weeds are the most costly, causing more than a third of the estimated worldwide annual economic damages, totalling US\$350 billion as a result of invasive species (Sheppard et al. 2003). Classical biological weed control involves the introduction of exotic natural enemies, such as insects (e.g. weevil), to reduce the abundance of a plant that has become an invader when spread outside of its native range. The aims of biological weed control are to achieve and maintain low weed population levels and to replace the weed with a more desirable plant (McEvoy and Cox 1991). Amongst different ways of controlling invasive plants, biological control is widely regarded as a safer and more suitable alternative than other forms of invasive species management (Ehler 1998; McFadyen 1998; Thomas and Willis 1998; Pemberton 2000). Hill and Greathead (2000) claimed that biological control is a highly cost effective means for controlling invasive weeds on a regional scale, compared to chemical control methods. However, biological control agents can have stochastic effects on the target plant because of the difficulties of establishing and adapting to the new environment. Some weeds can become resistant against mycoherbicides (Dixon et al. 1994; Reglinski et al. 1994; Lyon et al. 1995; Reglinski et al. 1997) or weevil (Giga et al. 1991; Ortiz et al. 1995; Derera et al. 2000). As a result, managers do not easily choose biological controls as other control measures (such as chemical and mechanical controls) can be more reliable.

The aim of this paper is to analyse whether biological control becomes a less attractive option when its stochastic effects are considered. We consider the invasive Californian thistle in pastures in New Zealand, which is currently causing considerable damage to the livestock sector. Using a stochastic dynamic programming model, it is analysed whether introducing weevil (*Apion onopordi*) or mycoherbicides (*Sclerotinia sclerotiorum*) is an efficient management strategy if their effects are stochastic. For a set of integrated control strategies, we evaluate which strategies result in the highest expected net benefits from the pasture when the effects of biological control on the growth rates and shoot densities of the weed are stochastic. To be more precise, the following research questions are raised. 1) Is it worth introducing the weevil (*Apion onopordi*) or mycoherbicides (*Sclerotinia sclerotiorum*) considering their costs and stochastic effects? 2) Which combination of control options is the optimal? 3) What are the possible costs involved if 'green' control strategies are to be adopted and chemicals to be excluded? and 4) Is eradication of the Californian thistle worth pursuing?

For comparable studies (stochastic) dynamic programming models have been used (see e.g. Pandey and Medd 1991; Higgins et al. 1997; Bulte and van Kooten 1999). This paper, however, makes new contributions to the previous studies in three aspects. Firstly, we

conduct a stochastic optimisation model with a discrete decision variable consisting of the 62 feasible combinations of integrated control strategies. In the studies mentioned above, either only a single decision variable or a few decision variable were analysed. In reality, however, the question is often not which level of a single control strategy to adopt, but which combination of feasible control options is most efficient. Secondly, a complication of our model set up is that some control options can be chosen on an annual basis, whereas others (for example, the introduction of the weevil) have to be introduced only once, after which it will remain active in the pasture. Thirdly, we focus on the stochastic efficacy of the biological control agent on the invasive plant, while the studies mentioned above mainly focus on the risk of biological control attack on the non-target species, and less attention has been given to the success of biological control management on controlling invasive species. Regarding the research question whether eradication of the Californian thistle is worth pursuing, Olson et al. (2002) claimed that if the expected growth rate of invasive species is greater than one, eradication of weed is a better control strategy than reducing weed density to a lower level. Given that the expected growth rate of the Californian thistle is greater than one, we examine whether eradication would also be optimal in our case.

In this paper, we first describe the study area and the control options that are available to limit the Californian thistle invasion. Secondly, the model is discussed in detail. Finally, we discuss the results and present possible policy scenarios.

### 3.2 Case study: Californian thistle in New Zealand

The Californian thistle (*Cirsium arvense*) is an aggressive perennial weed that is widespread on pastures, rangelands, and other agricultural land (Donald 1990, Morishita 1999; Skinner et al. 2000). This thistle affects both perennial and annual crops, and is considered as one of the “world’s worst weeds” (Friedli and Bacher 2001). New Zealand, which has a very diverse and valuable natural resource base, has been widely invaded by the Californian thistle, causing severe environmental damage (Bascand and Jowett 1982; Bourdôt et al. 2004). It has been estimated that these damages have caused millions of dollars to be lost annually (Harris 2002). It is, therefore, important to find an efficient control strategy to reduce these damages. We consider seven possible control options to control Californian thistle in New Zealand, some of which can be applied simultaneously. From the possible combinations, 62 feasible combinations of control options (from now on called ‘control strategies’) are considered in our analysis. The seven control options for controlling the thistle are the following.

**Applying MCPA.** MCPA ((4-chloro-2-methylphenoxy) acetic acid) is a systemic herbicide that gives temporary control, however it severely damages nitrogen-fixing clovers in pasture. This herbicide is one of the most effective ways of quickly reducing thistle shoot density and can therefore be important in increasing the yield of the pasture (Barrons 1969). In this study, benefits lost by removing clover are added to the price of MCPA.

**Applying MCPB.** MCPB ((4-chloro-2-methylphenoxy) butanoic acid) is closely related to MCPA, but does not damage clovers.

**Mowing in January.** Mowing is a mechanical option for controlling Californian thistle. In this method, the arms and knives of the machine remove the thistle's foliage, which results in reduced root growth and reduced shoot production (Bourdôt et al. 1998).

**Mowing in March.** This is like the previous option, but mowing now occurs in March.

**Intensified grazing.** Grazing animals, such as geese, goats, sheep and cattle, at sufficiently high intensity can control invasive species in rangelands. Sheep and goats are most commonly used for this purpose because they often eat plants rejected by cattle and horses. The grazing of weeds damages their physiology and controls their spread (Monaco et al. 2001) and has been proven to be effective against Californian thistle (Hartley et al. 1984). Intensified grazing is done at the beginning of the growing season when the thistle leaves are still soft. During the intensified grazing period, the number of animals exceeds the grazing capacity of the pasture, this therefore leads to a lack of forage for the animals. This forces the animal to graze at some unpalatable plants, such as the thistle.

**Biological control.** To control the Californian thistle, two biological agents are considered:

- *Introducing a weevil:* phytophagous insects that can be used to control weeds. They usually come from the native habitat of the weed and must be extensively tested to ensure that they will not attack plants other than those being targeted (Pemberton 2000). Such insects, once established, can often support their own growth and expansion. Here we consider the weevil, *Apion onopordi*, a putative biological control agent for Californian thistle that is considered for release in New Zealand. The effect of *Apion onopordi* on the growth rate, however, is stochastic, depending on external circumstances such as the environmental conditions of the site or interaction between species.
- *Applying mycoherbicides.* These are plant pathogens that can control weeds in a similar way to chemical herbicides (Charudattan 1991; Trujillo and Templeton 1981). While the fungus *Sclerotinia sclerotiorum* is under development as mycoherbicides for weed control in New Zealand, its stochastic effect on shoot densities remains an issue affecting its eventual commercialisation (G.W. Bourdôt and D. Leathwick unpublished data).

### 3.3. Model

Weed control decisions have to be made each year and the effects of these decisions on weed densities are subject to stochasticity. Therefore, we set up a model to determine the sequence of control strategies that maximises the present value of expected net returns obtained from the pasture. The path of weed densities and sequence of control strategies were analysed for a period of 40 years. At the beginning of each year, a control strategy was chosen based on the

known weed density at the end of the previous year, and based on the probability distribution of the efficacy of the weevil and mycoherbicides at reducing the thistle growth rate and density. The effect of the control strategies is observed only in the year of application except for the introduction of the weevil. Once the weevil has been introduced, it will remain active for the rest of the planning period, although with a stochastic effect. For the other strategies, it is assumed that their effects last only for one year and that they are applied in an optimal manner.

In this section, first a deterministic dynamic programming model will be presented assuming that the weevil and mycoherbicides have a deterministic effect on the growth and the density of the thistle. Secondly, this model will be extended by introducing the stochastic effects of the weevil and mycoherbicides into the model. The deterministic model is presented first to enable a clearer understanding of the stochastic model.

### 3.3.1 A Deterministic dynamic programming model

The objective of the deterministic model is to choose a sequence of control strategies that maximises the present value of a stream of annual net benefits,  $V_t$ . Decision variable  $u_t$  is a discrete variable and corresponds to the control strategy adopted in year  $t$ . The number of control strategies that a decision maker can choose is given by  $ns$ , where  $u_t \in \{1, \dots, ns\}$ . See Table A.3.1 in the Appendix and Section 3.3 for an overview of control strategies. Note that the set of control strategies  $CS$  can be subdivided into two subsets:  $CS^{NI} = \{1, \dots, ns^{NI}\}$  and  $CS^I = \{ns^{NI}+1, \dots, ns\}$ , with  $CS^{NI}$  being the set of strategies that do not include the introduction of the weevil, and  $CS^I$  being the set of strategies that do include the introduction of the weevil.  $ns^{NI}$  represents the number of strategies that do not include the introduction of weevil. Once, one of the strategies from set  $CS^I$  has been adopted, the decision maker can only choose from set  $CS^{NI}$  in the subsequent years as the insect will remain active.

The dynamic programming problem can be defined as finding the sequence of control strategies which maximises

$$V(w_0) = \max_{\{u_t\}_{t=1}^T} \left\{ \sum_{t=1}^T \delta^{t-1} B_t(w_t, u_t) \mid w_t = f(w_{t-1}, u_t), \forall t \in \{1, \dots, T\} \right\} \quad (3.1)$$

where  $w_t$  represents the density of the thistle at the end of year  $t$ ,  $\delta$  represents the discount factor and  $T$  the final year of the planning period. In order to be able to solve the model using backward induction, the Bellman equation for year  $t$ , as usually defined in dynamic programming, is introduced.

$$V_t(w_{t-1}) = \max_{u_t} \{ B_t(w_t, u_t) + \delta V_{t+1}(w_t) \mid w_t = f(w_{t-1}, u_t) \} \quad (3.2)$$



In equation (3.2) the future net benefit,  $V_{t+1}$ , is affected by the density of the thistle shoots at the end of year  $t$ ,  $w_t$ . The net benefits in year  $t$  are affected by the control strategy adopted in year  $t$ ,  $u_t$  and the shoot density resulting from applying this strategy.

The net annual benefits of the pasture  $B_t(w_t, u_t)$  in year  $t$ , are obtained from the following functions (Cousens 1985):

$$B_t(w_t, u_t) = H_t(w_t) - C_t(u_t) \quad (3.3)$$

with,

$$H_t(w_t) = \frac{S \cdot \gamma}{g} \left( 1 - \frac{\zeta \cdot w_t}{100 \cdot [1 + (\zeta \cdot w_t / \alpha)]} \right) \quad (3.4)$$

where,  $H_t(w_t)$  are the benefits obtained from the pasture with a weed density  $w_t$  and  $C_t(u_t)$  represents the costs of adopting control strategy  $u_t$ . In the benefit function, parameter  $S$  represents the monetary value of a livestock unit;  $g$  represents the amount of forage production used per livestock unit per year and  $\gamma$  represents the annual yield of dry matter ( $\text{kg/m}^2$ ) in the absence of the weed. The parameter  $\zeta$  represents the percentage of yield loss caused by Californian thistle shoots as the density of shoots approaches zero and  $\alpha$  represents the percentage loss in yield as the density of the Californian thistle shoots approaches infinity.

Population dynamics of the thistle as presented in equation (3.2) are explained by the following, regularly applied, logistic growth function (see e.g. Bacher and Friedli 2002):

$$w_t = L(u_t) \cdot r \cdot N(u_t) \cdot w_{t-1} \cdot \left( 1 - \frac{w_{t-1} \cdot N(u_t)}{\mu} \right) + w_{t-1} \cdot N(u_t) \quad (3.5)$$

where  $L(u_t)$  is a multiplier which indicates the effect of the control strategy,  $u_t$ , on the growth rate of the thistle.  $N(u_t)$  is a multiplier that indicates the direct effect of the control strategy on the thistle density (see Table A.3.1 in appendix for the values of these parameters). For instance, for the first strategy where none of the control strategies were chosen ( $u_t=1$ ), the value of  $N(u_t)$  and  $L(u_t)$  are equal to one, which means they have no effect on the benefit function. Control strategy number 11, for instance, reduces the growth rate to 70 percent of its initial value ( $L(11)=0.7$ ) and reduces the density of thistle to 18 percent of its initial value ( $N(11)=0.18$ ). Parameter  $\mu$  represents the maximum density of the Californian thistle shoots that can grow on one square metre of land. The value of  $\mu$  is constant and is not changed by control treatments. The parameter  $r$  represents the maximum rate of increase in Californian thistle shoot density and is influenced by the ecological conditions of a site. The introduction of the weevil is assumed to reduce the growth rate ( $r$ ) for all remaining years. No other control treatment changes the value of  $r$ . The impacts of the various control strategies and their costs are shown in Table A.3.1 in the appendix. Fig. 3.1 shows the relationship between the Californian thistle shoot densities in year  $t$  as a function of the density in year  $t+1$  in the

absence of any control treatment which follows from the logistic growth function (3.5). At a particular moment, thistle growth can be so large that the density exceeds carrying capacity for a short moment. If this happens, net growth will fall in the next period, resulting in a density at or below carrying capacity.

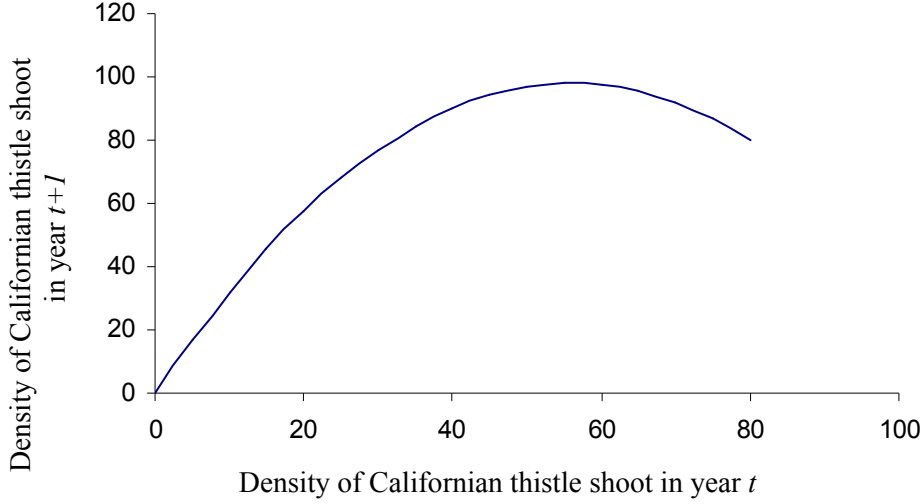


Fig. 3.1: The dynamics of Californian thistle. The density of the thistle shoots in year  $(t+1)$  is given as a function of shoot density in year  $t$  as described by Equation (5) without control.

### 3.3.2 The Stochastic dynamic programming model

In the deterministic model (3.2), the efficacy of the biological control agents (the weevil and mycoherbicides) was assumed to be constant. However, evidence shows that the effect of the biological agents on the host plant could be lower or higher as a result of a number of environmental factors or resistance of the host plants (Giga et al. 1991; Ortiz et al. 1995; Reglinski et al. 1997; Derera et al. 2000). In this section, the deterministic model has been extended as a result of including the stochastic effect of the biological control methods on the density and growth rate of the thistle.

The stochasticity adopted is based on two control options. Firstly, the weevil, *Apion onopordi*, has a stochastic effect on the growth rate of the thistle (multiplier  $L(u_t)$  in (3.5)). Secondly, the mycoherbicides, *Sclerotinia sclerotiorum* has a stochastic effect on the thistle density (multiplier  $N(u_t)$  in (3.5)). At the beginning of each period  $t$ , (knowing that thistle density at the end of the period is  $t-1$ ), a decision has to be made with respect to the control strategy,  $u_t$ . Due to the biological control methods having stochastic effects, benefits in year  $t$  as well as future benefits are stochastic.

To introduce the stochastic effects of the insect on the growth rate of the thistle, we introduce a stochastic multiplier,  $\Psi(u_t)$ , which indicates the effect of the control strategy on the growth rate. The mean and standard deviation of  $\Psi(u_t)$  depend on the control strategy  $u_t$  that is adopted. For the strategies  $u_t \in CS^{NI}$  that do not include the insect, there is no risk and therefore  $\Psi(u_t) = L(u_t)$ , as defined in (3.5). For strategies  $u_t \in CS^I$  that do include the insect, the exact effect on the growth rate of the thistle is uncertain beforehand, but the expected effect is assumed to be known and equal to  $E\Psi(u_t) = L(u_t)$ .

Similarly, to introduce the stochastic effect of mycoherbicides on the thistle density, we introduce a stochastic multiplier  $\Phi(u_t)$  which indicates the effect of the control strategy on the thistle density. For the strategies  $u_t$  that do not include mycoherbicides there is no stochasticity and  $\Phi(u_t) = N(u_t)$ , as defined in (3.5). For the strategies  $u_t$  which include mycoherbicides, the exact effect on thistle density is uncertain beforehand, but the expected effect is assumed to be known and equal to  $E\Phi(u_t) = N(u_t)$ .

Assume a situation with a discrete number of states of nature, each resulting in a different efficacy of the insect or mycoherbicides and each with a known probability of occurrence. For each period  $t$  there are  $I$  possible states of nature. For the strategies that include the stochasticity, each state of nature  $i \in \{1, \dots, I\}$  results in a different realisation of the stochastic multiplier. Introduce the parameters  $\psi_i(u_t)$  and  $\phi_i(u_t)$  which reflect the possible realisations of the growth rate multiplier  $\Psi(u_t)$  and density multiplier  $\Phi(u_t)$ , respectively (in the state of nature  $i$ ,  $\Psi(u_t) = \psi_i(u_t)$  or  $\Phi(u_t) = \phi_i(u_t)$ ). Now define the probabilities with which the multipliers take the values  $\psi_i(u_t)$  and  $\phi_i(u_t)$ .

$$\Pr(\Psi(u_t) = \psi_i(u_t)) = p_i^\psi \quad (3.6)$$

$$\Pr(\Phi(u_t) = \phi_i(u_t)) = p_i^\phi \quad (3.7)$$

For possible states of nature  $i \in \{1, \dots, I\}$ . It follows that:

$$\sum_{i=1}^I p_i^\psi = 1 \text{ and } 0 \leq p_i^\psi \leq 1 \quad (3.8)$$

$$\sum_{i=1}^I p_i^\phi = 1 \text{ and } 0 \leq p_i^\phi \leq 1 \quad (3.9)$$

Because the multipliers of the growth rate or the density are stochastic, thistle growth function (3.5) also becomes stochastic. Thistle density at the end of each period is a stochastic variable,  $W_t$ , depending on a given density level at the end of period  $t-1$ ,  $w_{t-1}$ . In the stochastic model we consider one stochasticity at a time; either the effect of the weevil is stochastic or the effect of mycoherbicides is stochastic. For the first case, possible realisations of  $W_t$  are:

$$w_{it} = \psi_i(u_t) \cdot r \cdot N(u_t) \cdot w_{t-1} \cdot \left(1 - \frac{w_{t-1} \cdot N(u_t)}{\mu}\right) + w_{t-1} \cdot N(u_t), \quad i \in \{1, \dots, I\} \quad (3.10)$$

If the effect of mycoherbicides is stochastic possible realisations of  $W_t$  are:

$$w_{it} = L(u_t) \cdot r \cdot \phi_i(u_t) \cdot w_{t-1} \cdot \left(1 - \frac{w_{t-1} \cdot \phi_i(u_t)}{\mu}\right) + w_{t-1} \cdot \phi_i(u_t), \quad i \in \{1, \dots, I\} \quad (3.11)$$

As a result of this set up, it is impossible to determine net benefits for each strategy at the beginning of period  $t$ . Only the present value of expected net benefits can be determined, which are represented in the following equation:

$$EV_t(w_{t-1}) = \underset{u_t}{\text{Max}} \left\{ EB_t(W_t, u_t) + \delta EV_{t+1}(W_t) \mid W_t \text{ given in (2.10)} \right\} \quad (3.12)$$

In the case in which the effect of the weevil is stochastic, the equation (3.12) is equal to:

$$EV_t(w_{t-1}) = \underset{u_t}{\text{Max}} \left\{ \sum_{i=1}^I p_i^{\Psi} (B_t(w_{it}, u_t) + \delta EV_{t+1}(w_{it})) \mid w_{it} \text{ given in (10)} \right\} \quad (3.13)$$

with  $w_{it}$  the density in period  $t$  if  $\Psi(u_t) = \psi_t(u_t)$ . For the case in which mycoherbicides have a stochastic effect, the equation is similar with  $p_i^{\Psi}$  replaced by  $p_i^{\phi}$  and  $w_{it}$  given by (3.11).

Because  $u_t$  is a discrete variable, it is not possible to solve the problem analytically. Therefore we solve the model numerically using backward induction. In the next section, how the model is solved is explained in further detail.

Parameter values used for solving model (3.13) are presented in Table 3.1 and Table A.3.1. Values reflect time steps of one year.

Table 3.1: Parameter values.\*

Parameter	Definition	Value
$\gamma$	Annual yield of dry matter (kg/m <sup>2</sup> )	8.5
$\alpha$	Percentage loss in yield as the density of the thistle shoots approaches infinity	100
$r$	Growth rate of the thistle	2.5
$\mu$	Maximum density of the thistle shoots that can grow on one square meter	80
$g$	Forage production used per livestock unit per year (kg)	550
$\varsigma$	Yield loss caused by the thistle as the density of shoots approaches zero (%)	5
$S$	Monetary value of a livestock unit (NZ\$)	68.3
$\delta$	Discount factor	0.97

\*  $\gamma, \alpha, r, \mu$  and  $\varsigma$  were obtained from personal communications (Bourdôt and Leathwick, 2006). Other parameters ( $g, S$  and  $\delta$ ) were calculated or obtained from financial budget manual (Burt, 2004).

Seven control options are considered that could be combined with each other. Table A.3.1 shows all of the feasible combinations (strategies) of these seven control options. The rows of this table represent the strategies and the columns show the control options adopted for each strategy. The columns indicate whether for a certain strategy the corresponding

option is included (a number one) or not (a zero). For instance, in strategy 1, in which all values of the row are zero, no control option was applied. In strategy 16, control options 2 and 5 were set to one and the others to zero, indicating that this strategy is a combination of MCPB and mowing in January.

All possible combinations of control options yield 128 potential strategies. From these strategies those that are illogical are excluded resulting in 62 feasible control strategies. For example, combining both types of herbicides MPCA and MPCB and mowing in January is illogical as firstly they have the same time of application and secondly there will be no additive effect of the combination.

To determine the (mean) values of the strategy efficacy multipliers  $N$  and  $L$ , each element of the control strategies was first allocated an efficacy (shown in row 2-8 in Table A.3.1), based on published data (Table A.3.1 appendix). For strategies with a combination of control options, the efficacies were taken from published data where available. In the absence of empirical data, the strategy efficacy values were calculated assuming that the actions of the component options were independent and multiplicative. For example, for strategy 9 (MCPA + mowing in January), the proportion of thistle shoots surviving both treatments was  $N = 0.26 \times 0.5 = 0.13$  (see Table A.3.1).

### 3.3.3 Probability distributions for the weevil and mycoherbicides efficacy

The effect of the weevil on thistle growth rate has a normal distribution with mean 0.7 (a reduction of the growth rate with 30%) and standard deviation 0.35. In order to avoid unrealistically low multiplier values or values exceeding 1 (which would imply that biological control would increase weed density) (G.W. Bourdôt and D. Leathwick unpublished data), a conditional normal distribution was adopted allowing only values of  $\psi_i(u_i)$  in the range [0.4, 1]. Following Hurrell et al. (2001) and Bourdôt et al. (2004), the efficacy of the mycoherbicides is assumed to have a log normal distribution with a minimum of 0.2, a maximum of 0.8, a mean of 0.6 and a standard deviation of 0.3. Note that the other control options considered could also have stochastic effects. As there is more evidence that efficacy of biological control is subject to stochasticity due to a large number of e.g. climatological conditions, we concentrate on this and leave an analysis of the other possible stochastic effects for future research. Considering them as well would not seriously complicate the approach adopted; however it would go beyond the scope of the current paper.

An often used method in stochastic models is to randomly draw a number of possible realisations of the stochastic variable from a continuous probability distribution. However this method has a disadvantage because each time the model is solved, the possible efficacies of biological control realisations give different values. This may lead to different results and makes it difficult to compare scenarios with each other. To solve this problem,  $I$  discrete

states of nature were introduced, (see above) each resulting in discrete values for the insect efficacy and each with a known probability of occurrence.

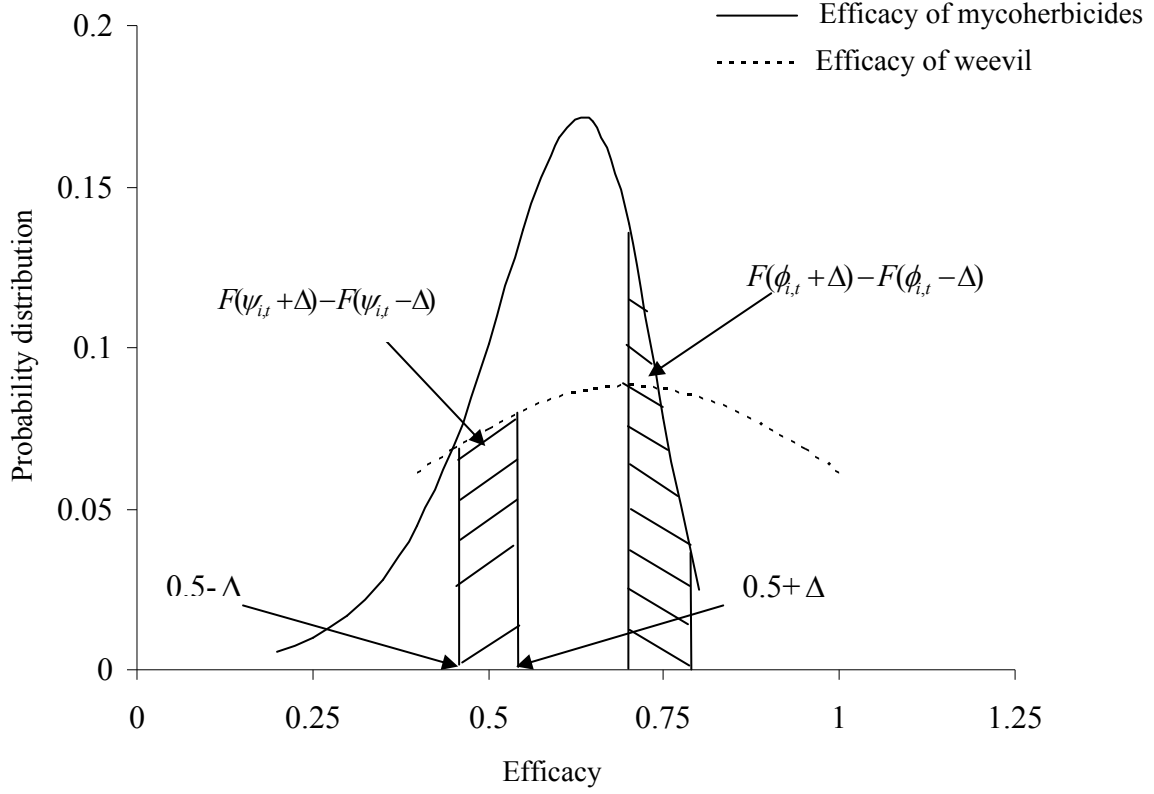


Fig.3.2: The probability distribution for efficacies of the weevil and mycoherbicide.

To derive from the continuous probability distribution of  $\Psi(u_t)$  and  $\Phi(u_t)$  the probability of occurrence for each state of nature, intervals of states of nature are considered in which multiplier values have a given value. A sensitivity analysis showed that the precision of the results does not change if the interval size becomes less than 0.05, which therefore is adopted as interval size. The probability that the state of nature is  $i$  and consequently the weevil efficacy is equal to  $\psi_i(u_t)$ , is equal to

$$p_i^\Psi = \Pr(\Psi(u_t) = \psi_i(u_t)) = \frac{F(\psi_i(u_t) + \Delta) - F(\psi_i(u_t) - \Delta)}{F(1) - F(0.4)} \quad (3.14)$$

with,

$$\Delta = \frac{\psi_i(u_t) - \psi_{i-1}(u_t)}{2} = 0.025 \text{ for } i \in \{2, \dots, I\} \quad (3.15)$$

with  $F$  the cumulative probability function of the normal distribution. In order to have a maximum cumulative probability of one,  $F(\psi_{it}(u_t) + \Delta) - F(\psi_{it}(u_t) - \Delta)$  is divided by  $F(1) -$

$F(0.4)$ . As a result (3.8) is satisfied. Table 3.2 represents the values of  $\psi_i$  and  $p_i^\psi$ , and Fig.3.2 shows the probability distribution for the weevil efficacy.

Table 3.2: The efficacies of the weevil and mycoherbicide and probabilities of their occurrence.

Efficacy of the weevil and probabilities of their occurrence		Efficacy of mycoherbicide and probabilities of their occurrence	
Efficacies ( $\psi_i$ )	Probabilities (%) $p_i^\psi = \Pr(\Psi = \psi_i)$	Efficacies ( $\phi_i$ )	Probabilities (%) $p_i^\phi = \Pr(\Phi = \phi_i)$
0.4	4.91	0.2	0.006
0.45	5.49	0.25	0.01
0.5	6.02	0.3	0.0168
0.55	6.46	0.35	0.0279
0.6	6.80	0.4	0.0448
0.65	7.01	0.45	0.0692
0.7	7.08	0.5	0.1.01
0.75	7.01	0.55	0.1365
0.8	6.8	0.6	0.1652
0.85	6.46	0.65	0.1704
0.9	6.02	0.7	0.1386
0.95	5.49	0.75	0.0783
1	4.91	0.8	0.0246

Similarly, the probability that mycoherbicides efficacy is equal to  $\phi_i(u_t)$  is equal to

$$p_i^\phi = \Pr(\Phi(u_t) = \phi_i(u_t)) = G(\phi_i(u_t) + \Delta) - G(\phi_i(u_t) - \Delta) \quad (3.16)$$

with,

$$\Delta = \frac{\phi_i(u_t) - \phi_{i-1}(u_t)}{2} = 0.025 \text{ for } i \in \{2, \dots, I\} \quad (3.17)$$

with  $G$  the cumulative probability function of the lognormal distribution. As a result (3.9) is satisfied. Fig.3.2 shows the probability distribution of mycoherbicides efficacy and Table 3.2 shows the values for  $\phi_i$  and  $p_i^\phi$ .

### 3.4 Results and Discussion

In this section, the effect of the stochastic efficacy of the weevil and the mycoherbicide on the control strategy chosen is discussed. To analyse these effects, three scenarios (see Table 3.3) were distinguished: no stochasticity, stochastic weevil efficacy and stochastic mycoherbicides efficacy. Furthermore, using chemicals as weed control options has the risk of contaminating food and water and causing damage to the environment. Therefore some users prefer not to apply them (Reid et al. 2007). As chemicals could be more cost-effective and beneficial from an economic point of view we wanted to evaluate the effect of excluding these control options on the net benefits of the pasture. Therefore, for each scenario, two sub-scenarios are considered (see Table 3.3).

Table 3.3: Definition of scenarios.

	With MCPA and MCPB	Without MCPA MCPB
Deterministic model	$D_C$	$D_{CN}$
Model with stochastic efficacy of weevil	$S_{w,C}$	$S_{w,CN}$
Model with stochastic efficacy of mycoherbicide	$S_{myc,C}$	$S_{myc,CN}$

In Scenario  $D_C$  and  $D_{CN}$  the efficacy of all control strategies are assumed to be known with certainty. Scenario  $S_{w,C}$  and  $S_{w,CN}$  represent the results of the stochastic model, in which the weevil introduction has a stochastic effect on thistle growth. Scenarios  $S_{myc,C}$  and  $S_{myc,CN}$  represent the stochastic model in which the efficacy of mycoherbicides is stochastic. In the aforementioned scenarios, index “C” refers to the sub-scenarios in which chemicals (MCPA and MCPB) are included and index “CN” refers to the sub-scenarios in which chemicals are not included. For all scenarios and sub-scenarios we compare the expected net present value (NPV) for the entire planning period ( $V_1(w_0)$  – see (3.12) or (3.13)) and the thistle density of the optimal strategies (see (3.10) or (3.11)).

The model is solved by MATLAB using backward induction. Depending on the scenario adopted, there is no stochasticity, the weevil efficacy is stochastic or mycoherbicides efficacy is stochastic. For each (sub)-scenario, the results of two models were compared: one in which the weevil is introduced in period 1 and one in which the weevil is not introduced at all. The optimal strategy is the strategy that results from the model giving the maximum net present value. Also considering the possibility of introducing the insect into any of the other periods is possible without much additional complication. Chalak-Haghighi et al. (2008b) show for a deterministic case that the weevil will always be adopted at the *first* period, irrespective of the starting density and for a large range of possible efficacy levels. For the case in which the



weevil is introduced in period 1 and weevil efficacy is stochastic, the backward induction algorithm as used in this paper is discussed in the Appendix (A3.1).

### 3.4.1 Transition of the thistle density between year $t$ and year $t+1$

The difference equation system of the state variable is autonomous which means that the state transition equation ((3.10) or (3.11)) does not depend on the time period. For each year, optimal control strategies only depend on the current thistle density and not on control strategies that were chosen in the previous period (except when the weevil is introduced, after which the thistle growth rate changes). Using the optimal decision rule provides an optimal state transition. For Scenario  $S_{myc,C}$  and  $S_{myc,CN}$  the optimal transition, i.e. the relationship between the state at time  $t$  and the state at time  $t+1$ , under optimal management is shown in Fig.3.3. Only these transition relationships are shown as all three scenarios show similar transitions. This similarity shows that the stochastic effect may change the type of control strategy and consequently the NPV, but its influence on the transition path of thistle densities is small. There are, however, some differences in thistle density when we compare the sub scenarios.

Fig.3.1 shows that without control treatments, the thistle population rapidly increases. In contrast, the optimal application of control strategies results in the maintenance of low thistle densities and a quick reduction of the density. Fig.3.3 shows for the sub scenarios with chemicals, that the density of thistle in year  $t+1$  is slightly higher in these scenarios than in the sub-scenarios without chemicals, when the initial density of the thistle is lower than 50 shoot/m<sup>2</sup>. For initial densities exceeding 50 the reverse is true. By excluding chemicals more control options are needed. For higher densities, however, chemicals are more cost effective and can more easily keep the thistle density at a lower level.

As we can see in Fig.3.3, in contrast to Olson et al. (2002) densities will never reach zero, even though they will become small in only few years. Olson et al. (2002) assume that control reduces invasive species growth with a fixed number instead of a percentage reduction as assumed in our case. As a result, in our study no strategy reduces thistle density to zero, which we consider more realistic for the case in New Zealand.

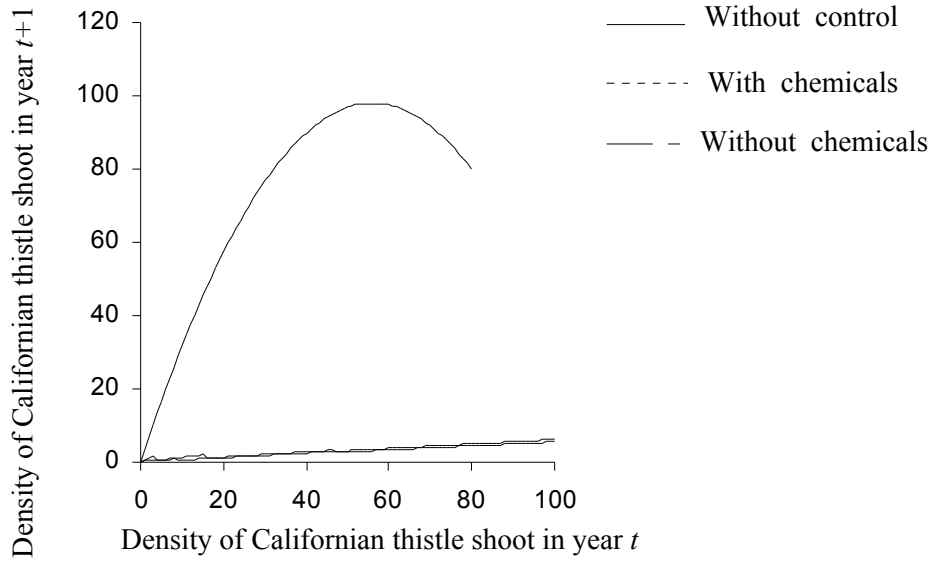


Fig.3.3: The probability distribution for efficacies of the weevil and mycoherbicide.

### 3.4.2 Optimal Strategies

The optimal strategies for the different scenarios are presented in Table 3.4. As can be seen from this table, the optimal strategies for Scenario  $D_C$  and  $S_{w,C}$  are similar, as well as those for Scenario  $D_{CN}$  and  $S_{w,CN}$ . In other words, a stochastic effect of the weevil on the thistle growth rate does not change the optimal control option adopted. Even though the target plants can become resistant to the weevil (Giga et al. 1991; Ortiz et al. 1995; Derera et al. 2000) and its efficacy is stochastic, the costs of introducing weevil are so low as compared to other control options, that it is introduced in the first period for all scenarios and also the choice of its introduction does not affect the other control options being part of the optimal control strategy. Moreover, weevil is the only control option which once introduced can compensate a low efficacy in one year with a possible high effect in another year. These results are in contrast to some arguments against the introduction of the weevil, as some argue that the weevil is not worth introducing because of its stochastic efficacy. Its low costs and long-run effect, however, make it a very attractive control option as long as it is not causing an excessive negative external effect to the ecosystem.

Table 3.4 also shows that mycoherbicides will be adopted at a higher thistle density when its efficacy is stochastic (density of 61 for Scenario  $S_{myc,C}$  and density of 8 for Scenario  $S_{myc,CN}$ ) as compared to the deterministic case (density of 49 for Scenario  $D_C$  and density of 3 for Scenario  $D_{CN}$ ). The main reason for this is that when the stochastic efficacy of mycoherbicides is considered, the possibility that mycoherbicides have a low efficacy is taken into account. Mycoherbicides is an expensive option and results show that for densities below 61 (Scenario  $S_{myc,C}$ ) or 8 (Scenario  $S_{myc,CN}$ ) this option is not cost-effective. In Scenario  $S_{myc,CN}$  where chemical are excluded, applying mycoherbicides is optimal at a lower thistle density than Scenario  $S_{myc,C}$ .

where the chemicals are included. Because chemicals are cost effective options to control the thistle and in their absence mycoherbicides replace them at a lower density level to keep the thistle density low. Despite of the risk of resistance to mycoherbicides (Dixon et al. 1994; Reglinski et al. 1994; Lyon et al. 1995; Reglinski et al. 1997) the results show that this option is still optimal for densities exceeding 61 (Scenario  $S_{myc,C}$ ) or 8 (Scenario  $S_{myc,CN}$ ).

Table 3.4: Optimal starting strategies for different ranges of initial thistle density for the deterministic model and stochastic models. Chemicals are either included or excluded .\*

Initial Californian Thistle  density (shoots/m <sup>2</sup> )	With chemicals		Without chemicals	
	Scenario $D_C$		Scenario $D_{CN}$	
	Number	Strategy	Number	Strategy
0.00-1	8	Insect	8	Ins.
1-3	39	Ov.Gr., Ins.	40	Mo.J. Ov.Gr., Ins.
3-5	14	MCPA, Ov.Gr., Ins.	29	Myc., Mo.J., Ov.Gr., Ins.
5-17	14	MCPA, Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
17-49	15	MCPA, Mo.J. Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
49-100	55	MCPA, Myc., Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
	Scenario $S_{w,C}$		Scenario $S_{w,CN}$	
	Number	Strategy	Number	Strategy
0.00-1	8	Insect	8	Ins.
1-3	39	Ov.Gr., Ins.	40	Mo.J. Ov.Gr., Ins.
3-5	14	MCPA, Ov.Gr., Ins.	29	Myc., Mo.J., Ov.Gr., Ins.
5-17	14	MCPA, Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
17-49	15	MCPA, Mo.J. Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
49-100	55	MCPA, Myc., Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
	Scenario $S_{myc,C}$		Scenario $S_{myc,CN}$	
	Number	Strategy	Number	Strategy
0.00-1	8	Insect	8	Ins.
1-3	39	Ov.Gr., Ins.	40	Mo.J. Ov.Gr., Ins.
3-5	14	MCPA, Ov.Gr., Ins.	40	Mo.J., Ov.Gr., Ins.
5-8	14	MCPA, Ov.Gr., Ins.	36	Mo.M., Mo.J., Ov.Gr., Ins.
8-17	14	MCPA, Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
17-61	15	MCPA, Mo.J. Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.
61-100	55	MCPA, Myc., Ov.Gr., Ins.	62	Myc.,Mo.M. Mo.J., Ov.Gr., Ins.

\*Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), Ov.Gr. (overgraze), Ins. (weevil).

In Table 3.4<sup>†</sup>, the optimal strategies are given for ranges of possible initial densities of the thistle. Two observations can be made from this. Firstly, the higher the initial thistle density the more control options are needed to keep thistle density at an optimal level. For high densities, the economic damages of the thistle are higher than the costs of additional control options, due to which strategies with more control options are optimal. Secondly, for the sub scenarios without chemicals ( $D_{CN}$ ,  $S_{w,CN}$  and  $S_{myc,CN}$ ) more than one control option is needed to substitute for the chemical control option. Chemical application is more effective than the non-chemical control options. Thirdly results show that mycoherbicides are good

<sup>†</sup> In this chapter, the optimal control strategies are introduced at slightly different thistle densities as compared to the last chapter. This is due to the use of different packages (GAMS and MATLAB) in the two chapters.

alternative for the use of MCPA and MCPB. In the sub scenarios without chemicals, mycoherbicides are applied at a much lower density levels than in sub scenarios with chemicals, even when stochasticity is included.

The NPVs (NZ\$/ha) for the various scenarios for a range of initial densities of thistle are presented in Table 3.5. Comparing the NPV of the stochastic and deterministic model, it can be seen that when the stochastic effect of mycoherbicides is included in the model, a marginally lower NPV is obtained from the pasture. In the stochastic model the reduction of the NPV for low efficacies outweighs the increase of the NPV for high efficacies due to the non-linearity in the model. Table 3.5 also shows that when chemicals are excluded from the control strategies a slightly lower NPV is obtained. This reduction in NPV becomes larger as thistle density increases. As explained above, for higher densities of thistle, chemicals become more cost effective.

Table 3.5 shows that effects of excluding chemicals on the NPV are low. It can be concluded that replacing chemicals by more environmentally friendly options can be done at relatively low costs.

Table 3.5: NPV(NZ\$/ha) for selected initial thistle densities for the deterministic model and stochastic models. Chemicals are either included or excluded .\*

Initial Californian thistle density	NPV when chemicals are included (NZ\$/ha)	NPV when chemicals are excluded (NZ\$/ha)	Percentage decrease in NPV when chemicals are excluded
	Scenario $D_C$	Scenario $D_{CN}$	
1	23341	23341	0
5	23170	22987	0.8
10	23119	22877	1.1
20	23039	22724	1.4
40	22952	22578	1.6
60	22880	22476	1.8
80	22821	22394	1.9
	Scenario $S_{w,C}$	Scenario $S_{w,CN}$	
1	23341	23341	0
5	23170	22987	0.8
10	23119	22877	1.1
20	23039	22724	1.4
40	22952	22578	1.6
60	22880	22476	1.8
80	22821	22394	1.9
	Scenario $S_{myc,C}$	Scenario $S_{myc,CN}$	
1	23288	23288	0
5	23124	22996	0.6
10	23077	22890	0.8
20	22998	22790	0.9
40	22912	22657	1.1
60	22834	22556	1.2
80	22773	22477	1.3

### 3.4.3 Sensitivity Analysis

We conducted a sensitivity analysis to examine the effects of variations of parameter values on the optimal strategy chosen. Table 3.6 shows for which range of parameter values the optimal control strategies do not change. Of course NPV slightly changes if parameter values change.

Table 3.6: Parameter deviations (%) and the range of their change that do not affect the optimal strategy.\*

Parameter	Deviations (%)	Range
$\gamma$	18	6.9-10
$\alpha$	50	50-100
$r$	8	2.3-2.7
$\mu$	40	48-112
$g$	20	440-660
$\zeta$	20	4-6
$S$	20	55-89
$C$	15	Depend on the strategy
N 1	10	Depend on the strategy
N 2	40	Depend on the strategy
L	14	Depend on the strategy

\*  $\gamma$  (annual yield of dry matter ( $\text{kg/m}^2$ )),  $\alpha$  (percentage loss in yield as the density of the thistle shoots approaches infinity),  $r$  (growth rate of the thistle),  $\mu$  (maximum density of the thistle shoots that can grow on one square meter),  $g$  (forage production used per livestock unit per year ( $\text{kg}$ )),  $\zeta$  (Yield loss caused by the thistle as the density of shoots approaches zero(%)).  $S$  (monetary value of a livestock unit (NZ\$)),  $\delta$  (discount factor), N 1 (density efficacy for strategies 2-8), N2 (density efficacy of a single control option within the control strategies 9-62) and L (growth rate efficacy).

The sensitivity analysis shows that firstly the growth rate of the thistle has the strongest effect on the results because the growth rate directly influences thistle density, which has a large impact on the benefit obtained from the pasture. Secondly, most of the non-economic parameters such as  $\gamma$ ,  $\alpha$ ,  $\mu$ ,  $g$ , and  $\zeta$ , that are influenced by conditions of the site, have a low impact on the strategy chosen. Thirdly, efficacies of the control options have a low impact on the strategy chosen. This impact is lower when the control option is combined with other options, because when one control option is combined with other options, variation is absorbed by the other control options. For example the application of MCPA alone reduces the thistle density by 74 percent (strategy number 2) but when it is combined with mycoherbicides, mowing in March and over grazing (strategy number 53) the additive efficacy of MCPA is only 4.2 percent. Fourthly, variations in the economic parameters ( $C$  and  $\delta$ ) have a very low effect on the strategy chosen. In the model, the discount factor ( $\delta$ ) has a negligible impact because most control strategies only have a one year effect, and show immediate effects. The only strategy that have an effect for longer time periods, the weevil, is

relatively cheap and also has a strong effect from the moment of introduction. As a result, weevil will always be introduced in period one and the discount rate only has a minor effect. From this we conclude that the model is robust against changes in the parameter values.

### 3.5 Implication of results for management of the thistle

We obtained a solution to an invasive species management problem which considered the stochastic effect of biological control treatments. We applied a stochastic dynamic programming approach for controlling Californian thistle in pastures in New Zealand. This model helps us to answer the research questions as raised in the introduction. Regarding the question whether it would be worth to introduce the weevil (*Apion onopordi*) if its stochastic effects were considered, we found that despite of the possible stochastic efficacy, it remains optimal to introduce the weevil to the pastures in New Zealand, assuming they have no adverse effect on other species. Regarding the question whether it would be worthwhile to introduce mycoherbicides (*Sclerotinia sclerotiorum*) if its cost and stochastic effects were considered, we can conclude that despite of the possible stochastic effect of mycoherbicides, it is worth applying mycoherbicides when the density of the thistle is more than 61 shoot/m<sup>2</sup> when chemicals are included and 8 shoot/ m<sup>2</sup> when chemicals are excluded. It is also concluded that if stochasticity would not have been considered, farmers would have introduced it already at a lower thistle density. Regarding the question which combination of control options is optimal, the analysis indicates that when chemicals are included, for most ranges of thistle densities (densities between 5 to 61 shoot/m<sup>2</sup>) the best control strategies are to apply MCPA, intensified grazing and introduction of weevil in period 1 (number 14) and MCPA, mowing in January, intensified grazing and introduction of weevil in period 1 (number 15). It is also shown that when chemicals are excluded, for most densities (densities more than 8 shoot/m<sup>2</sup>), the best strategy is to apply mycoherbicides, mowing in January, mowing in March, intensified grazing and introduction of weevil in period 1 (number 62). Regarding the question on the possible costs if we exclude chemicals, the model shows that excluding chemicals and using more environmentally friendly options reduce NPV by a maximum of only 1.3 percent. Finally, regarding to the question whether eradication is worth pursuing, the results show that total eradication, as found to be optimal by Olson et al. (2002), is not possible for our case due to the model set up. As there are no control options that would allow for total eradication, Olson's conclusions are rather theoretical.

Furthermore, the results show that the stochasticity of the weevil efficacy does not affect the optimal control strategy adopted. Furthermore mycoherbicides will only be adopted at a higher level of weed density if we take the stochastic effect of mycoherbicides into account. Our analysis demonstrates how stochastic dynamic programming offers a useful framework for management of invasive species that include stochastic parameters.

## **Acknowledgments**

We are grateful to Dr Graeme Bourdôt and Dave Leathwick for providing valuable data. We thank Prof. Anton Meister for providing contacts and facilities at Massey University in New Zealand. We thank Elena Saiz and Eligius Hendrix for their valuable comments on the programming in MATLAB. Funds were provided from Wageningen University and Iranian Ministry of Research, Science and Technology.

### A3.1 Appendix

In this appendix, the set up of applied backward induction algorithm in MATLAB is explained. Assume that weevil is introduced in period 1 and that the weevil efficacy is stochastic. Introduce the following sets:

$$\begin{aligned}
 CS &= \{1, \dots, ns\} - \text{all feasible control strategies} \\
 CS^{NI} &= \{1, \dots, ns^{NI}\} - \text{all feasible control strategies that do not include weevil} \\
 CS^I &= \{ns^{NI}+1, \dots, ns\} - \text{all feasible control strategies that do include weevil} \quad (A3.1) \\
 Wt &= \{1, \dots, nw\} - \text{set giving indices for the possible densities at the beginning of a period} \\
 I^n &= \{1, \dots, I\} - \text{set giving indices for the possible states of nature.}
 \end{aligned}$$

First, introduce the vectors and matrices needed to be able to determine the optimal strategies. Introduce the  $nw$ -vector  $\mathbf{h}$  containing a discrete number of possible densities at the beginning of a certain period. Elements  $h_w$  reflect the possible densities at the beginning of a certain period that are considered for the analysis, with  $w \in \{1, \dots, nw\}$ . Vector  $\mathbf{h}$  is ordered in such a way that  $h_1$  is the lowest density possible ( $h_1=0$ ) and  $h_{nw}$  the maximum density possible (for our choice of parameters  $h_{nw}=100$ ). Next, the  $ns$ -vector  $\mathbf{N}$  is introduced giving for each possible strategy  $u \in CS$  the effect of  $u$  on thistle density. Moreover, introduce  $I$ -vectors  $\boldsymbol{\psi}$  and  $\mathbf{p}^\psi$ . Elements  $\psi_i$  give the efficacies with which weevil affect the thistle growth rate for state of nature  $i \in I^n$ . Note that vector  $\boldsymbol{\psi}$  is independent of  $u$  as it is assumed here that weevil is introduced in the beginning of the first period and remains active for all periods in the planning period. Elements  $p_i^\psi$  give the probabilities of occurrence of state of nature  $i \in I^n$ . Introduce the  $nw \times ns^{NI} \times I$ -matrix  $\mathbf{W}^{NI}$  and the  $nw \times (ns - ns^{NI}) \times I$ -matrix  $\mathbf{W}^I$ . Matrix  $\mathbf{W}^{NI}$  indicates for each density level  $h_w$ , for  $w \in Wt$ ,  $u \in CS^{NI}$ , and  $i \in I^n$  what will be the density at the end of period  $t$  if the weevil has already been introduced in one of the previous periods and therefore the thistle growth rate is stochastic. Similarly,  $\mathbf{W}^I$  gives for each  $w \in Wt$ ,  $u \in CS^I$ , and  $i \in I^n$  what will be the density at the end of period  $t$  in case weevil will be introduced in that period. The matrices can be derived as follows – see (3.10):

$$W_{w,u,i}^{NI} = \psi_i \cdot r \cdot N_u \cdot h_w \cdot \left(1 - \frac{h_w \cdot N_u}{\mu}\right) + h_w \cdot N_u, \text{ for } w \in Wt, u \in CS^{NI}, i \in I^n \quad (A3.2)$$

$$W_{w,u,i}^I = \psi_i \cdot r \cdot N_u \cdot h_w \cdot \left(1 - \frac{h_w \cdot N_u}{\mu}\right) + h_w \cdot N_u, \text{ for } w \in Wt, u \in CS^I, i \in I^n \quad (A3.3)$$

Note that (A3.2) and (A3.3) are the same, except for the control strategies that can be adopted.

Next, introduce the  $nw \times ns^{NI} \times I$ -matrix  $\mathbf{B}^{NI}$  and the  $nw \times (ns - ns^{NI}) \times I$  matrix  $\mathbf{B}^I$ . Each element of these matrices contains the benefits in a certain year if the density at the beginning of the year is  $h_w$ , with  $w \in Wt$ , a control strategy  $u \in CS^{NI}$  (for  $\mathbf{B}^{NI}$ ) or  $u \in CS^I$  (for  $\mathbf{B}^I$ ) is adopted and you are in state of nature  $i \in I^n$ . They are derived as follows:



$$B_{w,u,i}^{NI} = \frac{S \cdot \gamma}{g} \left( 1 - \frac{\varsigma \cdot W_{w,u,i}^{NI}}{100 \cdot \left[ 1 + \frac{\varsigma \cdot W_{w,u,i}^{NI}}{\alpha} \right]} \right) - C_{w,u}, \text{ for } w \in Wt, u \in CS^{NI}, i \in I^n \quad (A3.4)$$

$$B_{w,u,i}^I = \frac{S \cdot \gamma}{g} \left( 1 - \frac{\varsigma \cdot W_{w,u,i}^I}{100 \cdot \left[ 1 + \frac{\varsigma \cdot W_{w,u,i}^I}{\alpha} \right]} \right) - C_{w,u}, \text{ for } w \in Wt, u \in CS^I, i \in I^n \quad (A3.5)$$

Equations (A3.2)-(A3.5) give us the necessary ingredients to derive, using backward induction, the optimal path of control strategies and the optimal present value of expected net benefits. Two  $nw \times T$ -matrices **EV** and **U** are set up. Each element  $EV_{wt}$  contains the expected net benefits from period  $t$  until the end of the planning period if the density at the beginning of period  $t$  is  $h_w$ . Each element  $U_{wt}$  contains the optimal control strategy for period  $t$  if the density at the start of period  $t$  is  $h_w$ .

First, the  $T^{th}$  column of matrix **EV** and **U** are determined. For the final period  $T$ , for each  $w \in Wt$  the strategy  $u \in CS^{NI}$  will be determined which maximizes expected net benefits for period  $T$ :

$$EV_{wT} = \text{Max}_{u \in CS^{NI}} \left\{ \sum_{i \in I} p_i^\psi \cdot B_{w,u,i}^{NI} \right\} \quad (A3.6)$$

$$U_{wT} = \text{ArgMax}_{u \in CS^{NI}} \left\{ \sum_{i \in I} p_i^\psi \cdot B_{w,u,i}^{NI} \right\} \quad (A3.7)$$

Next, the  $T-1^{th}$  columns of matrix **EV** and **U** are determined. A complicating factor is that if in the beginning of period  $T-1$  weed density is equal to  $h_w$ , with  $w \in Wt$ , and strategy  $u \in CS^{NI}$  is adopted, the weed density at the beginning of period  $T$ ,  $W_{w,u,i}^{NI}$  is not necessarily (or most likely not) an element of **h**. In (A3.6), however, only for the densities with levels  $h_w$ , optimal strategies have been determined and most likely not for a density  $W_{w,u,i}^{NI}$ . Therefore, the optimal expected net benefits obtained in period  $T$  if the density at the beginning of that period is equal to  $W_{w,u,i}^{NI}$  is estimated using interpolation. For that purpose, define  $h^-$  and  $h^+$ , as the two elements from vector **h** for which  $[h^-, h^+]$  is the smallest range for which  $h^- \leq W_{w,u,i}^{NI} \leq h^+$ . Similar to (A3.6) and (A3.7), for the period  $T-1$ , for each  $w \in Wt$  the strategy  $u \in CS^{NI}$  will be determined which maximizes expected net benefits until the end of the planning period – see (3.13):

$$EV_{w,T-1} = \underset{u \in CS^{NI}}{\text{Max}} \left\{ \sum_{i \in I} p_i^\psi \cdot \left[ B_{w,u,i}^{NI} + \delta \cdot \left\{ V_{h^-,T} \cdot \left( \frac{h^+ - h}{h^+ - h^-} \right) + V_{h^+,T} \cdot \left( \frac{h - h^-}{h^+ - h^-} \right) \right\} \right] \right\} \quad (\text{A3.8})$$

$$U_{w,T-1} = \underset{u \in CS^{NI}}{\text{ArgMax}} \left\{ \sum_{i \in I} p_i^\psi \cdot \left[ B_{w,u,i}^{NI} + \delta \cdot \left\{ V_{h^-,T} \cdot \left( \frac{h^+ - h}{h^+ - h^-} \right) + V_{h^+,T} \cdot \left( \frac{h - h^-}{h^+ - h^-} \right) \right\} \right] \right\} \quad (\text{A3.9})$$

A similar reasoning can be followed for all remaining periods  $t \in \{T-2, \dots, 2\}$  with  $T-1$  replaced by  $t$  and  $T$  replaced by  $t+1$ . In each period  $t$ , the elements of the  $(t+1)^{\text{st}}$  column of matrix  $\mathbf{EV}$  are used to determine the optimal expected net benefits from period  $t$  till  $T$ . Finally, for period 1, the model is more or less similar, but with some small differences in control strategies that can be chosen and definitions of net benefits. For period 1,

$$EV_{w,1} = \underset{u \in CS^I}{\text{Max}} \left\{ \sum_{i \in I} p_i^\psi \cdot \left[ B_{w,u,i}^I + \delta \cdot \left\{ V_{h^-,2} \cdot \left( \frac{h^+ - h}{h^+ - h^-} \right) + V_{h^+,2} \cdot \left( \frac{h - h^-}{h^+ - h^-} \right) \right\} \right] \right\} \quad (\text{A3.10})$$

$$U_{w,1} = \underset{u \in CS^I}{\text{ArgMax}} \left\{ \sum_{i \in I} p_i^\psi \cdot \left[ B_{w,u,i}^I + \delta \cdot \left\{ V_{h^-,2} \cdot \left( \frac{h^+ - h}{h^+ - h^-} \right) + V_{h^+,2} \cdot \left( \frac{h - h^-}{h^+ - h^-} \right) \right\} \right] \right\} \quad (\text{A3.11})$$

Table A.3.1. Controlling strategies, their efficacy and costs. The values of N and L were calculated from published data when available (see "Source" column), or were estimated by GWB<sup>‡</sup> and DL<sup>§</sup> when published data was not available. Costs, C, were obtained from Fleming et. al. (2003). Myc (mycoherbicide), Mo.M (mow in March), Mo.J (mow in January), Ov.Gr. (overgraze), Ins (*Apion onopordi*).

Strategy	Control options							Efficacy			Source
	1 MC PA	2 MC PB	3 Myc c.	4 Mo. M.	5 Mo. J.	6 Ov. Gr.	7 Ins.	N	L	Cost \$NZ/h a	
1	0	0	0	0	0	0	0	1.00	1	0	
2	1	0	0	0	0	0	0	0.26	1	90.8	Hartley et al. (1984)
3	0	1	0	0	0	0	0	0.28	1	98	Hartley et al. (1984)
4	0	0	1	0	0	0	0	0.40	1	115	Hurrell et al.(2001)
5	0	0	0	1	0	0	0	0.57	1	75	Bourdôt et al..(1998)
6	0	0	0	0	1	0	0	0.50	1	75	Bourdôt et al..(1998)
7	0	0	0	0	0	1	0	0.29	1	34	Hartley et al. (1984)
8	0	0	0	0	0	0	1	0.68	0.7	3	Friedli and Bacher(2001)
9	1	0	0	0	1	0	0	0.13	1	165.8	GWB and DL
10	1	0	0	0	0	1	0	0.08	1	124.8	GWB and DL
11	1	0	0	0	0	0	1	0.18	0.7	93.8	GWB and DL
12	1	0	0	0	1	1	0	0.04	1	199.8	GWB and DL
13	1	0	0	0	1	0	1	0.09	0.7	168.8	GWB and DL
14	1	0	0	0	0	1	1	0.05	0.7	127.8	GWB and DL
15	1	0	0	0	1	1	1	0.03	0.7	202.8	GWB and DL
16	0	1	0	0	1	0	0	0.14	1	173	GWB and DL
17	0	1	0	0	0	1	0	0.08	1	132	Hartley et al. (1984)
18	0	1	0	0	0	0	1	0.19	0.7	101	GWB and DL
19	0	1	0	0	1	1	0	0.04	1	207	GWB and DL
20	0	1	0	0	1	0	1	0.10	0.7	176	GWB and DL
21	0	1	0	0	0	1	1	0.06	0.7	135	GWB and DL
22	0	1	0	0	1	1	1	0.03	0.7	210	GWB and DL
23	0	0	1	0	1	0	0	0.20	1	190	GWB and DL
24	0	0	1	0	0	1	0	0.12	1	149	GWB and DL
25	0	0	1	0	0	0	1	0.27	0.7	118	GWB and DL
26	0	0	1	0	1	1	0	0.06	1	224	GWB and DL
27	0	0	1	0	1	0	1	0.14	0.7	193	GWB and DL
28	0	0	1	0	0	1	1	0.08	0.7	152	GWB and DL
29	0	0	1	0	1	1	1	0.04	0.7	227	GWB and DL
30	0	0	0	1	1	0	0	0.29	1	150	Bourdôt et a..(1998)
31	0	0	0	1	0	1	0	0.17	1	109	GWB and DL
32	0	0	0	1	0	0	1	0.39	0.7	78	GWB and DL
33	0	0	0	1	1	1	0	0.08	1	184	GWB and DL
34	0	0	0	1	1	0	1	0.20	0.7	153	GWB and DL
35	0	0	0	1	0	1	1	0.11	0.7	112	GWB and DL
36	0	0	0	1	1	1	1	0.06	0.7	187	GWB and DL
37	0	0	0	0	1	1	0	0.15	1	109	GWB and DL
38	0	0	0	0	1	0	1	0.34	0.7	78	GWB and DL
39	0	0	0	0	0	1	1	0.20	0.7	37	GWB and DL
40	0	0	0	0	1	1	1	0.10	0.7	112	GWB and DL
41	1	0	1	0	0	0	0	0.10	1	205.8	GWB and DL
42	0	1	1	0	0	0	0	0.11	1	213	GWB and DL
43	0	0	1	1	0	0	0	0.23	1	190	GWB and DL
44	1	0	1	0	1	0	0	0.05	1	280.8	GWB and DL
45	1	0	1	0	0	1	0	0.03	1	239.8	GWB and DL
46	1	0	1	0	0	0	1	0.07	0.7	208.8	GWB and DL
47	0	1	1	0	1	0	0	0.06	1	288	GWB and DL
48	0	1	1	0	0	1	0	0.03	1	247	GWB and DL
49	0	1	1	0	0	0	1	0.08	0.7	216	GWB and DL
50	0	0	1	1	1	0	0	0.11	1	265	GWB and DL
51	0	0	1	1	0	1	0	0.07	1	224	GWB and DL
52	0	0	1	1	0	0	1	0.16	0.7	193	GWB and DL
53	1	0	1	0	1	1	0	0.02	1	314.8	GWB and DL
54	1	0	1	0	1	0	1	0.04	0.7	283.4	GWB and DL
55	1	0	1	0	0	1	1	0.02	0.7	242	GWB and DL
56	0	1	1	0	1	1	0	0.02	1	322	GWB and DL
57	0	1	1	0	0	1	1	0.02	0.7	250	GWB and DL
58	0	0	0	1	1	1	1	0.06	0.7	187	GWB and DL
59	0	0	1	1	1	1	0	0.03	1	299	GWB and DL
60	0	0	1	1	1	0	1	0.08	0.7	268	GWB and DL
61	0	0	1	1	0	1	1	0.01	0.7	227	GWB and DL
62	0	0	1	1	1	1	1	0.02	0.7	302	GWB and DL

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<sup>§</sup> Leathwick, D.



## On the risk of extinction of a wild plant species through spillover of a biological control agent: analysis of an ecosystem compartment model

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**ABSTRACT**

Invasive plant species can be controlled by introducing one or more of their natural enemies (insect herbivores) from their native range; however such introduction entails the risk that the introduced natural enemy will attack indigenous plant species in the area of introduction. Here we study the effect of spillover of a natural enemy from a managed ecosystem compartment (agriculture) in the area of introduction to a natural compartment (non-managed) in which an indigenous plant species is attacked by the introduced natural enemy, whereas another indigenous plant species, which competes with the first, is not attacked. The combination of competition and herbivory may result in extinction of the attacked wild plant species. Using a modelling approach, we determine important model parameters that characterize the risk of extinction. Risk factors include: (1) a high attack rate of the introduced enemy on the wild non-target species; (2) factors favouring large spillover from the managed ecosystem compartment to the natural compartment; these include a moderately *low* attack rate of the introduced enemy on the target species, enabling large resident populations of the insect herbivore in the managed compartment and high dispersal; (3) niche overlap expressed as stronger competition between the attacked non-target species and its competitor(s). These findings point to the importance of spillover and the relative attack rates (specificity) of introduced natural enemies with respect to target and non-target plant species.

**Key words**

Biological control, Invasive species, Dispersal; Spillover, Extinction risk, Ecosystem compartment model, Herbivory, Competition

## 4.1 Introduction

Invasive plant species pose a great problem to global agriculture and ecosystems, threatening valuable indigenous species and productivity in agricultural and natural systems (Callaway and Aschehour 2000; Pimentel 2002b; Sheppard et al. 2003). Classical biological control, i.e. the introduction of natural enemies from the native range of the invasive species, is widely regarded as a safe and suitable form to manage invasive species (Ehler 1998; Thomas and Willis 1998; Pemberton 2000;). Classical biological control can be highly costs effective and avoids the use of herbicides (Charudattan 2001). Chalak-Haghighi et al. (2008a) has recently shown that an insect herbivore (*Apion onopordi*) can increase the net present value obtained from the pasture by reducing the growth rate of Californian thistle (*Cirsium arvense*).

An important issue in biological control is whether the imported natural enemies may attack non-target species. An important issue in biological control is whether these may attack non-target species. Many authors have discussed the environmental risks of the introduction of natural enemies for classical biological control (e.g. Thomas and Willis 1998; Follett and Duan 1999; Wajnberg et al. 2001). In order to assess this risk we need to understand the ecological dynamics of biological control agent in the ecosystems where they are introduced, and their interactions with other species. These interactions include both local population interactions as well as spatial processes, e.g. spillover of enemies from one ecosystem compartment to another.

Mobility of biological control agents allows them to penetrate to remote native habitats (Henneman and Memmott 2001). Many of the biological control agents introduced for pest control in agricultural areas can feed on alternative host plants in natural habitats and are likely to disperse between agricultural and natural systems (Symondson et al. 2002; Rand et al. 2006; Wirth et al. 2007). These natural enemies can produce large negative effects in the natural habitats by their spillover or cross-edge invasion effects (Suarez at al. 1998; Cronin and Reeve 2005; Rand et al. 2006). For instance, adult beetles of the corn rootworm (*Diabrotica* ssp), which feed in agricultural land as larvae, largely spill over into tall-grass prairie causing damage to native plants (McKone et al. 2001).

Before introducing a natural enemy to a managed system it is important to consider potential spillover effects to the natural environment, resulting in attack on endangered or protected species in the natural environment. For instance, a herbivore (*Rhinocyllus conicus*) was introduced to biologically control Platte thistle (*Cirsium canescens*) in the United States. After dispersal it attacked a protected and rare relative, the Pitcher's thistle (*Cirsium pitcheri*) (Louda et al. 2003; Louda et al. 2005).

Because ecological conditions of the managed and natural systems can differ, many different plant species interactions (e.g. competition) can prevail in managed and natural systems. Herbivores can disperse fast or slow between the systems, which affects the

dynamics of species in both systems due to spillover. Currently, the conditions under which dispersal of a biological control agent from a managed to a natural system occurs which produces a spillover effect threatening biodiversity, are not systematically analyzed and more work is needed to enable comprehensive assessments of risk (Rand et al. 2006).

This paper aims at analysing how a biological control agent that is introduced to reduce an invasive weed species in an agricultural system can affect a wild plant species' risk of extinction. For this, we use a modelling approach to elucidate risks of introduction of an insect herbivore species for biological controlling the weed in agriculture. The model includes key processes such as the interaction between a herbivore and its target and non-target plant species, dispersal of the enemy from one ecosystem compartment to another, and the competitive relationships between a non-target species and other species in a natural compartment. The objective is to identify those system characteristics that enhance or mitigate the risk of extinction of the non-target plant species in the natural compartment, and provide greater insight in the interrelationships between the different dynamic processes involved. In the next section the model system is described, followed by the mathematical analysis. Next, a numerical analysis is presented and finally, conclusions are drawn.

## 4.2 Description of the model system

For our analysis we model our system as two compartments: 1) a managed compartment where locally a herbivore ( $z_m$ ) is introduced to control a pest weed ( $w$ ), and 2) a natural compartment where the same herbivore species (here denoted as  $z_n$ ) can attack a wild plant species (species  $x$ ) (Fig. 4.1). The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment, herbivores attack a non-target host plant species ( $x$ ) which competes with another plant species or group of species ( $y$ ). There have been some studies on two compartment model system. Vellend et al. (2003), for instance, studies plant range expansion system. Pond et al. (1998), used a two compartment model to study age dependence distribution of animals. Differently from others we consider the main processes in the model as herbivory, competition and dispersal.

Without the insect herbivore, the two compartments (see Fig. 4.1) would be strictly separated: the weed in the managed compartment does not influence the coexisting competing plant species in the natural compartment. However, when the herbivore is introduced, the systems are linked through dispersal of the herbivore. The link between species  $w$  (the weed) and  $x$  (the non-target wild species) can be characterized as apparent competition; they share a common herbivore (Holt 1977). It is assumed that the initial situation in the natural compartment is characterized by stable equilibrium, i.e. individuals of each of the competing species have less competitive effect on the other species than on their own; they have sufficient niche differentiation to enable coexistence (Begon et al. 1996).



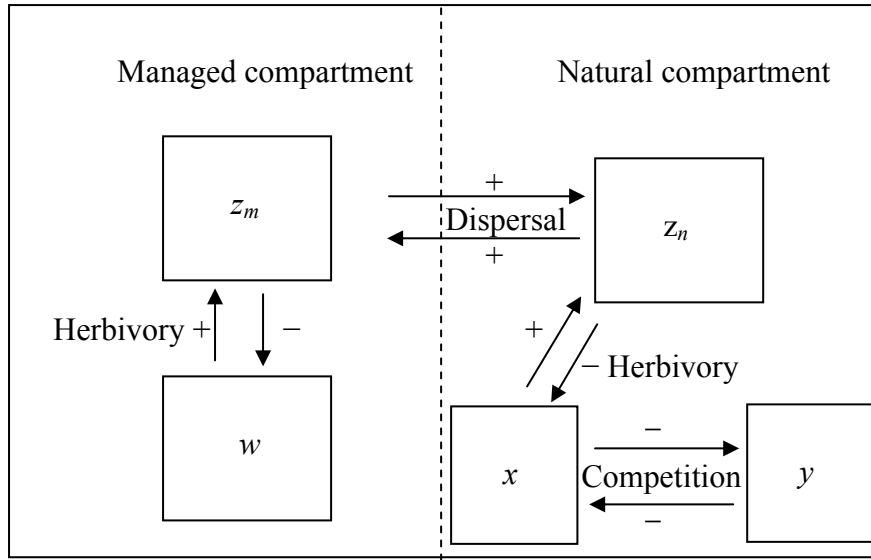


Fig. 4.1: Schematic representation of the modelled system. Introduction of a herbivore to the managed compartment (e.g. pasture) suppresses the weed population ( $w$ ). Herbivores disperse between the compartments. They feed on a wild plant species ( $x$ ), which is in competition with one or more other plant species ( $y$ ). The subpopulations of the herbivore in the managed compartment and in the natural compartment are denoted as  $z_m$  and  $z_n$  respectively.

The arrival of a herbivore in the natural compartment, where it is assumed to attack only one of the competing plant species, *viz*  $x$ , can offset the initially stable equilibrium between  $x$  and  $y$ . The competing species  $y$  can profit and increase in density. The non-target host plant,  $x$ , might go extinct due to the combination of herbivory and competition. The suppressive effect of herbivores on the wild non-target plant species could be further aggravated by sustained spillover of the herbivore from the managed compartment.

The dispersal of the herbivore influences both its own local densities and that of its host plant species ( $x$  and  $w$ ) in both compartments. Net dispersal of herbivores is always to the compartment with a lower density, and a compartment with higher host plant density produces more herbivores. The weed can produce a large population and substantial spillover of herbivores to the natural compartment.

In the full system complex interactions between species exist. A mathematical analysis and numerical exploration and sensitivity analysis of our model are used to elucidate these interactions.

The dynamics of the weed,  $w$ , is modelled with a logistic growth equation:

$$\frac{dw}{dt} = wr_w \left( 1 - \frac{w}{k_w} \right) \quad (4.1)$$

where  $r_w$  is the growth rate of the weed, and  $k_w$  represents the carrying capacity of the weed. All model parameters and state variables are listed in Table 4.1.

Table 1. An overview of default parameter values and state variables

Variable	Unit	Default Value	Explanation
$x$	shoot $\text{m}^{-2}$	None	Density of species $x$
$y$	shoot $\text{m}^{-2}$	None	Density of species $y$
$w$	shoot $\text{m}^{-2}$	None	Density of species $w$
$z_n$	$\text{m}^{-2}$	None	Density of herbivores in the natural compartment
$z_m$	$\text{m}^{-2}$	None	Density of herbivores in the managed compartment
Parameter			
$r_x$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $x$
$k_x$	shoot $\text{m}^{-2}$	80	Carrying capacity of plant species $x$
$a_{xy}$	None	0.8	Competition coefficient of species $y$ with respect to species $x$
$b_x$	$(\text{shoot } \text{m}^{-2})^{-1} \text{yr}^{-1}$	0.01	Attack rate of the herbivore $z$ on plant species $x$
$r_y$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $y$
$k_y$	shoot $\text{m}^{-2}$	80	Carrying capacity of plant species $y$
$a_{yx}$	None	0.8	Competition coefficient of species $x$ with respect to species $y$
$r_w$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $w$
$k_w$	shoot $\text{m}^{-2}$	80	Carrying capacity of plant species $w$
$b_w$	$(\text{shoot}/\text{m}^2)^{-1} \text{yr}^{-1}$	0.01	Attack rate of the herbivore $z$ on plant species $w$
$f$	$z \text{ shoot}^{-1}$	10	Fecundity coefficient of the herbivore
$q$	$\text{yr}^{-1}$	4	Relative death rate of the herbivore
$d$	$\text{yr}^{-1}$	0.5	Dispersal coefficient of the herbivore

The dynamics of the weed after introduction of the herbivore is modelled as:

$$\frac{dw}{dt} = wr_w \left( 1 - \frac{w}{k_w} \right) - b_w z_m w \quad (4.2)$$

where  $b_w$  represents the attack rate or the instantaneous hazard rate per unit of time ( $\text{yr}^{-1}$ ) that one individual of species  $z_m$  successfully encounters one shoot of weed.

The competitive interaction between plant species  $x$  and  $y$  in the natural compartment is modelled as a standard Lotka-Volterra competition system (e.g. Begon et al. 1996):

$$\begin{cases} \frac{dx}{dt} = r_x x \left( 1 - \left( \frac{x + ya_{xy}}{k_x} \right) \right) \\ \frac{dy}{dt} = r_y y \left( 1 - \left( \frac{y + xa_{yx}}{k_y} \right) \right) \end{cases} \quad (4.3a \text{ and } b)$$

where  $x$  and  $y$  are the two competing species. Their carrying capacities are denoted as  $k_x$ ,  $k_y$ , and their intrinsic growth rates as  $r_x$  and  $r_y$ . The per capita effect of species  $y$  on species  $x$  is  $a_{xy}$ , and  $a_{yx}$  denotes the reciprocal effect.

The following Lotka-Volterra competition model represents the dynamics of species  $x$  and  $y$  after the herbivore has reached the natural compartment

$$\begin{cases} \frac{dx}{dt} = r_x x \left( 1 - \left( \frac{x + y a_{xy}}{k_x} \right) \right) - b_x z_n x \\ \frac{dy}{dt} = r_y y \left( 1 - \left( \frac{y + x a_{yx}}{k_y} \right) \right) \end{cases} \quad (4.4a \text{ and } b)$$

where  $b_x$  represents the attack rate or instantaneous hazard rate per unit of time ( $\text{yr}^{-1}$ ) that one individual of species  $z_n$  successfully encounters one shoot of species  $x$ .

The dynamics of the herbivore in both the managed and the natural compartment is modelled as a Lotka-Volterra equation for predators, including metapopulation dynamics:

$$\begin{cases} \frac{dz_n}{dt} = f b_x x z_n - q z_n + d (z_m - z_n) \\ \frac{dz_m}{dt} = f b_w w z_m - q z_m + d (z_n - z_m) \end{cases} \quad (4.5a \text{ and } b)$$

where  $z_m$  respectively  $z_n$  represent the densities of herbivores in the managed and natural compartment,  $d$  is the dispersal rate of herbivores between the two compartments,  $f$  (fecundity coefficient) measures the number of herbivores that can be produced by removing one shoot of their host plant. The term  $f b_x x z_n$  represents the herbivore's birth rate and  $q$  represents the mortality rate of the herbivore.

The system dynamics are thus completely described with five equations (4.2, 4.4a, 4.4b, 4.5a and 4.5b), containing 13 parameters:  $b_w, b_x, k_w, k_x, k_y, r_w, r_x, r_y, a_{xy}, a_{yx}, f, q$  and  $d$  (Table 4.1).

### 4.3 Mathematical analysis

We analysed the complete 5-dimensional system to obtain all its equilibrium solutions explicitly and to determine their stability. Its non-dimensionalization (see appendix) reduces the number of parameters from 13 (Table 4.1) to nine. Moreover, the combinations of original parameters into the new parameters help us to see which changes in original parameter values have similar effects on the equilibrium values and the stability of the equilibria.

Table 4.2: The steady states  $(\bar{X}, \bar{Y}, \bar{Z}_n, \bar{Z}_m, \bar{W})$  of the non-dimensionalized system

Name	$(\bar{X}, \bar{Y}, \bar{Z}_n, \bar{Z}_m, \bar{W})$	Stability	Description/ comment
(i) Trivial equilibrium (Combine conditions <b>Ia</b> , <b>IIa</b> , <b>Va</b> and no insects present)	$(0,0,0,0,0)$	Unstable	All species extinct
(ii) Single species equilibrium 1 Combine conditions <b>Ib</b> , <b>IIa</b> , <b>Va</b> and no insects present)	$(1,0,0,0,0)$	Unstable	$x$ is at its carrying capacity
(iii) Single species equilibrium 2 (Combine conditions <b>Ia</b> , <b>IIb</b> , <b>Va</b> and no insects present)	$(0,1,0,0,0)$	Unstable	$y$ is at its carrying capacity
(iv) Single species equilibrium 3 (Combine conditions <b>Ia</b> , <b>IIa</b> , <b>Vb</b> and no insects present)	$(0,0,0,0,1)$	Unstable	$w$ is at its carrying capacity
(v) Two species equilibrium 1 (Combine conditions <b>Ib</b> , <b>IIa</b> , <b>Vb</b> and no insects present)	$(1,0,0,0,1)$	Unstable	both $x$ and $w$ are at their carrying capacity (no interaction)
(vi) Two species equilibrium 2 Combine conditions <b>Ia</b> , <b>IIb</b> , <b>Vb</b> and no insects present)	$(0,1,0,0,1)$	Unstable	both $y$ and $w$ are at their carrying capacity (no interaction)
(vii) Equilibrium 1 with only competition (Combine conditions <b>Ib</b> , <b>IIb</b> , <b>Va</b> and no insects present)	$(\frac{1-\beta}{(1-\beta\delta)}, \frac{1-\delta}{(1-\beta\delta)}, 0,0,0)$	Unstable for a large range of parameter values	no herbivores; $x$ and $y$ in their stable competition equilibrium; $w$ extinct
(viii) Equilibrium 2 with only competition (Combine conditions <b>Ib</b> , <b>IIb</b> , <b>Vb</b> and no insects present)	$(\frac{1-\beta}{(1-\beta\delta)}, \frac{1-\delta}{(1-\beta\delta)}, 0,0,1)$	Unstable for a large range of parameter values	no herbivores; $x$ and $y$ in their stable competition equilibrium; $w$ at its carrying capacity

Name	$(\bar{X}, \bar{Y}, \bar{Z}_n, \bar{Z}_m, \bar{W})$	Stability	Description/ comment
(ix) Managed compartment only (Combine conditions <b>Ia</b> , <b>IIa</b> , <b>Vb</b> and insects present)	$(0, 0, \frac{\mu(1-\bar{W})}{\eta(1+\zeta)}, \mu(1-\bar{W}), \bar{W})$	Unstable for a large range of parameter values	With $\bar{W} = \frac{\zeta + \zeta(1+\zeta)}{\varepsilon(1+\zeta)}$ ; species $x$ and $y$ extinct
(x) Managed compartment and species $y$ (Combine conditions <b>Ia</b> , <b>IIb</b> , <b>Vb</b> and insects present)	$(0, 1, \frac{\mu(1-\bar{W})}{\eta(1+\zeta)}, \mu(1-\bar{W}), \bar{W})$	Depending on the parameter values	With $\bar{W} = \frac{\zeta + \zeta(1+\zeta)}{\varepsilon(1+\zeta)}$ ; species $x$ extinct and $y$ at its carrying capacity (no interaction between compartments)
(xi) Natural compartment only (species $y$ extinct) (Combine conditions <b>Ib</b> , <b>IIa</b> , <b>Va</b> and insects present)	$(\bar{X}, 0, \alpha(1-\bar{X}), \frac{\eta\alpha}{(1+\zeta)}, (1-\bar{X}), 0)$	Unstable for a large range of parameter values	With $\bar{X} = \frac{\zeta + \zeta(1+\zeta)}{g(1+\zeta)}$ species $w$ and $y$ extinct (no interaction between compartments)
(xii) Natural compartment only (Combine conditions <b>Ib</b> , <b>IIb</b> , <b>Va</b> and insects present)	$(\bar{X}, 1-\delta\bar{X}, \alpha\left(\frac{1-\beta-(1-\beta\delta)}{\bar{X}}\right), \frac{\eta\alpha(1-\beta-(1-\beta\delta))\bar{X}}{(1+\zeta)}, 0)$	Unstable for a large range of parameter values	With $\bar{X} = \frac{\zeta + \zeta(1+\zeta)}{g(1+\zeta)}$ species $w$ extinct (no interaction between compartments)
(xiii) Implicit equation (Combine conditions <b>Ib</b> , <b>IIa</b> , <b>Vb</b> and insects present)	$(\bar{X}_1, 0, \bar{Z}_{n1}, \bar{Z}_{m1}, \bar{W}_1)$	Unstable for a large range of parameter values	Extinction of species $y$
(xiv) Implicit equation (Combine conditions <b>Ib</b> , <b>IIb</b> , <b>Vb</b> and insects present)	$(\bar{X}_2, \bar{Y}_2, \bar{Z}_{n2}, \bar{Z}_{m2}, \bar{W}_2)$	Depending on the parameter values	Possibly positive for all 5 species

We found at least 14 biologically relevant equilibria for the non-dimensionalized system, and these are listed in Table 4.2. In the second part of the appendix we derived the conditions to get equilibria, and the combinations of these conditions are given in Table 4.2. Equilibrium **i**, where all state variables are zero, is trivial. There are three equilibria with a single non-zero state variable (**ii**, **iii** and **iv**), three equilibria with two non-zero state variables (equilibria **v**, **vi** and **vii**), three equilibria with three non-zero state variables (**viii**, **ix**, and **xi**), and three equilibria with four non-zero state variables (**x**, **xii**, and **xiii**). There is a single equilibrium (**xiv**) in which all five species can coexist. However, it should be noted that the combination leading to **xiv** also can give not biologically relevant (i.e. negative) equilibrium solutions.

We are interested in stable equilibrium solutions of the system. For a locally stable equilibrium (attractor) all eigenvalues of the Jacobian matrix in that equilibrium should be negative (Edelstein-Keshet 1988). When an equilibrium is unstable, a small movement away from the equilibrium increases in the course of time. This can eventually lead to the extinction of one or more species. Note that the stability in a lower dimensional system (e.g. only 2 species) does not imply stability of the 5-dimensional system with only the two aforementioned species present. For instance Begon et al. (1995) suggest that interaction of only two competing plant species (e.g.  $x$  and  $y$ ), can result in a stable equilibrium if  $\beta$  and  $\delta < 1$  (see appendix). But equilibria **vii** and **viii** are unstable for a large set of parameter values for our system (system 6) even when  $\beta$  and  $\delta < 1$ . Because a small introduction of herbivores ( $z_m$  and/or  $z_n$ ) or weed can attract the existing equilibrium to a new equilibrium where  $z_m$ ,  $z_n$  or the weed get a positive value. For all equilibria except (**i-vi**) the derivation of the sign of all eigenvalues is not possible, even though we simplified the model by non-dimensionalization. Thus, we were not able to get explicit expressions for all equilibria and their stability. In the remainder of this paper, we therefore, use a numerical analysis to explore the characteristics of the equilibria.

#### 4.4. Numerical analysis

The numerical analysis shows that most equilibria are unstable for a wide range of parameter values. From the application point of view, the first 6 equilibria (equilibria **i-vi** in Table 4.2) with no herbivores are irrelevant, because we have introduced herbivores and assumed that they have established. Only two equilibria are of particular interest: 1) an equilibrium in which all species coexist (a positive solution for **xiv**), and 2) an equilibrium in which species  $x$  goes extinct because of the herbivores attack (equilibrium **x**). A trajectory that starts close to the positive equilibrium **xiv** and connects to equilibrium **x** is of special interest because it allows us to investigate which parameters are forcing plant species  $x$  to extinction. In the model, species  $x$  can reach a stable steady state where it gets a zero or negative growth after introduction of herbivores, because  $x$  is suppressed by two forces: 1) competition with  $y$ , and 2) herbivory by  $z_n$ .

Below we explore the parameter space and determine which of these two equilibria can occur, and give figures in which the dependency of equilibrium solution on parameter values are shown. In these figures only stable equilibria are represented. The results of the sensitivity analysis are only given for a selection of parameters that we consider most relevant. We exclude presentation of other results from our sensitivity analysis because they can be easily understood from the presented results and the relationship between parameters driven from non-dimensionalized system (see appendix). Note that cases where no stable coexistence of species  $x$  and  $y$  is possible before introduction of the herbivore are not included.

Parameter values for numerical illustration of the behaviour of the system are based on expert estimation by the authors and literature data; they represent loosely a system of thistle species with a weevil species as herbivore (Table 4.1). All three species ( $x$ ,  $y$ , and  $w$ ) have in the base case a relative growth rate of  $0.3 \text{ yr}^{-1}$  and a carrying capacity of  $80 \text{ shoots m}^{-2}$  (Schwinning and Parsons 1999; Chalak-Haghighi 2008a). The attack coefficients of the herbivore species on the weed and the wild species are  $0.01 (\text{shoot/m}^2)^{-1} \text{ yr}^{-1}$ . Competitive coefficients of both species are taken to be 0.8, representing a situation in which the species have rather similar resource requirements and niche overlap. The fecundity coefficient of the herbivore is 10 herbivores per shoot, and its death rate is  $4 \text{ yr}^{-1}$ . Finally, the dispersal coefficient is  $0.5 \text{ yr}^{-1}$ .

To illustrate the response of the system to parameter changes, and to identify factors that are related to extinction risk of the desired wild plant species,  $x$ , we first look at single parameter changes, notably in the coefficients for inter-plant competition, the attack coefficients, and the dispersal coefficient. Next, some of the combined effects of changes in parameters are illustrated.

The effect of the competition coefficient of  $y$  on wild plant species  $x$ ,  $a_{xy}$ , is illustrated first. As  $a_{xy}$  increases, the equilibrium density of  $x$  goes down, while that of  $y$  goes up (Fig. 4.2A). When the competition coefficient becomes larger than 1,  $x$  is outcompeted by  $y$ , which conforms to results from the Lotka-Volterra competition model. These changes in the densities also affect the density of the herbivore in both system compartment.

When  $a_{xy}$  increases, the density of the enemy goes down in the natural compartment, due to the decrease in host plant density,  $x$ . However, the enemy population is hardly affected in the managed compartment, because here, the density of the natural enemy is maintained by its feeding on the weed. Due to spillover of enemies from the managed compartment to the natural compartment, however, an increase in  $a_{xy}$  causes a slight decrease in the density of the enemy in the managed compartment. This slight decrease in  $z_m$  causes a small increase in weed density. Mutatis mutandis, an increase in  $a_{yx}$  has very similar effects (Fig. 4.2B). The example clearly demonstrates spillover and apparent competition effects (between  $x$  and  $w$ ), and it shows that the risk of extinction, expectedly, increases when the desired wild species has a strong competitor, i.e.  $a_{xy}$  is large. All the densities represented in the figures represent long term steady states that reflect stable equilibria for the pertinent parameter values. For

instance, the transition from a system with  $x$  to a system without  $x$  for  $a_{xy} > 1$  in Fig. 4.2A corresponds to a change from equilibrium (xiv) to equilibrium (x) (Table 4.2).

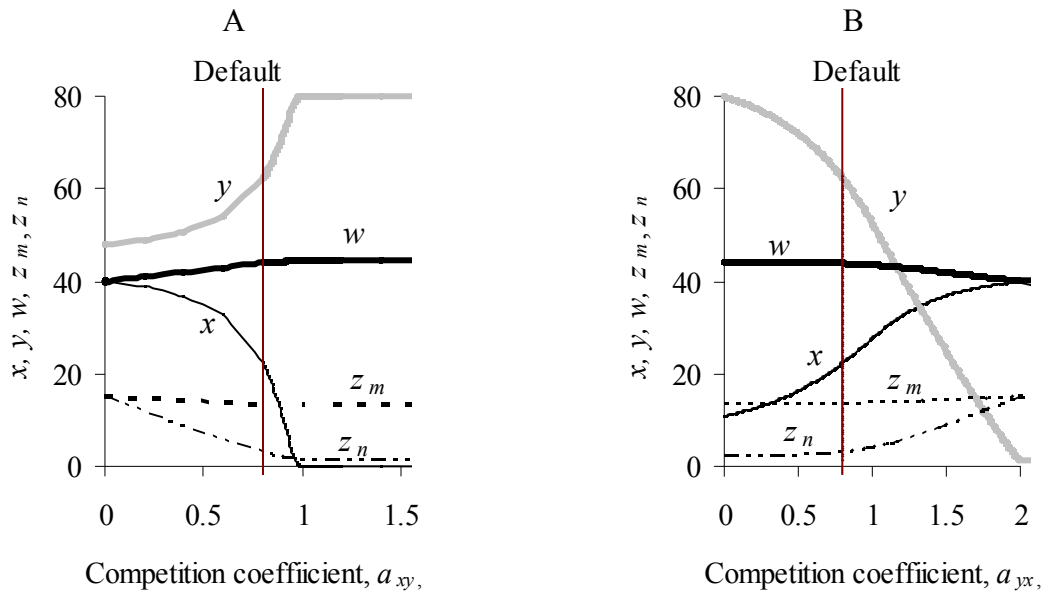


Fig. 4.2: The relationship between the equilibrium densities of wild host plant species ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartment ( $z_m$  and  $z_n$ ) and weed ( $w$ ) on the one hand and

(A) the plant competition coefficient  $a_{xy}$  that expresses the influence of species  $y$  on species  $x$  or (B) the plant competition coefficient  $a_{yx}$  that expresses the influence of species  $x$  on species  $y$ . The vertical lines shows the default value for  $a_{xy}$  and  $a_{yx}$ , all other parameter are at their default values.

The effects of  $k_x$  and  $k_y$  can be deduced from the illustrated effects of  $a_{yx}$  and  $a_{xy}$ . As shown in the appendix (non dimensionalization), the ratio  $k_y/k_x$  has the same fundamental influence on system dynamics as  $a_{xy}$ , while the ratio  $k_x/k_y$  has the same fundamental influence on system dynamics as  $a_{yx}$ .

The effect of the attack coefficient  $b_x$  is straightforward. As this coefficient increases,  $x$  goes down and  $y$ , released from competition by  $x$ , goes up (Fig. 4.3A). Enemy density shows an optimum response to the attack coefficient, a behaviour well-known from Lotka-Volterra predator-prey models (Fig. 4.3A). At low  $b_x$ , the enemy is not finding many host plants, and thus has little effect on the host population, and maintains only a very small population itself. As the attack coefficient goes up, the enemy population increases, while the host plant population decreases, up to a point where the decrease in the host population backfires and the enemy population decreases again. In the chosen two-compartment system, the slight peak in the enemy population at intermediate  $b_x$  results in a *reduction* of the spillover from the managed to the natural compartment, thus increasing herbivory pressure on the weed in the managed compartment and reducing, slightly, its density.



Changes in the attack coefficient  $b_w$  on the weed in the managed compartment have somewhat more complicated consequences. For low values of  $b_w$ , there is no discernible effect on the weed. Equilibrium densities of  $z_m$  and  $z_n$  are low when  $b_w$  is low at the chosen parameter values, due to insufficient encounter with host plant. When  $b_w$  increases, natural enemy densities increase, similarly as seen with an increase in  $b_x$ , up to a point where the host is overexploited, and natural enemy densities go down again. As  $b_w$  is becoming large enough to enable significant population of  $z_m$ , the density of the weed decreases, and due to spillover of the enemy from the managed to the natural compartment, the desired wild species,  $x$ , is also reduced in density, which then releases  $y$  from competition by  $x$ , and increases its density.

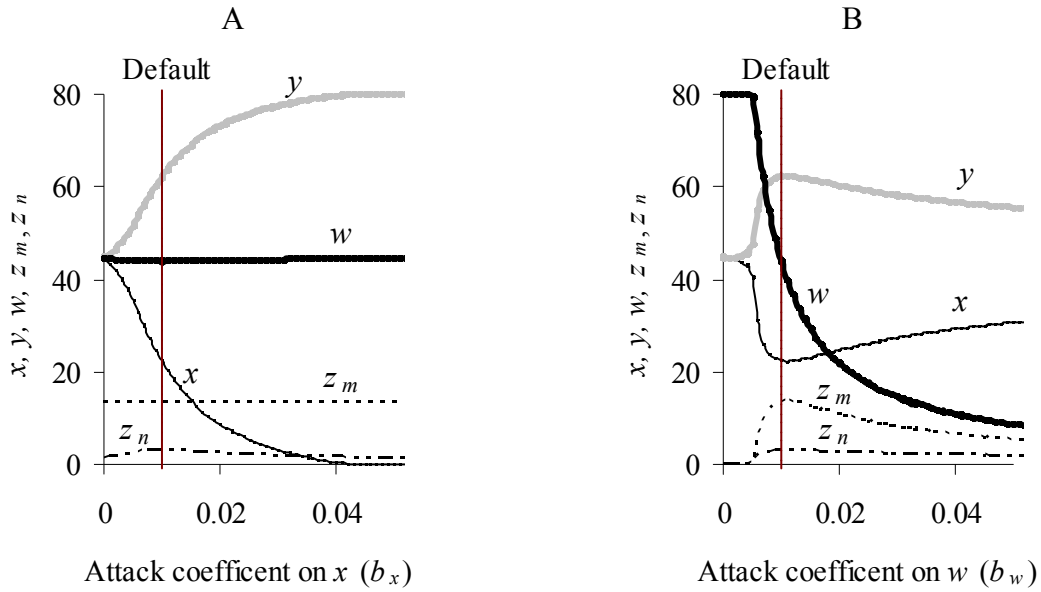


Fig. 4.3: The relationship between herbivore attack coefficients of herbivores on plant species ( $b_x$  and  $b_w$ ) and the equilibrium densities of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed compartment ( $z_m$ ), herbivores in the natural compartment ( $z_n$ ), weed ( $w$ ).

(A) herbivore attack coefficient  $b_x$  on species  $x$  and

(B) herbivore attack coefficient  $b_w$  on species  $w$ .

Vertical lines represent the default values for  $b_x$  and  $b_w$ , other parameter are set at their default values.

The interplay between  $b_x$  and  $b_w$  is further illustrated in Fig. 4.4, showing relationships between the equilibrium density of  $x$  and the attack rate of the enemy on  $x$  for different values of the attack rate of the enemy on the weedy species in the other compartment. When the attack rate on the weed is 0.01, the spillover effect is maximal, resulting in the minimum amount of  $x$ . For greater and for smaller values of  $b_w$  the equilibrium values of  $x$  are higher.

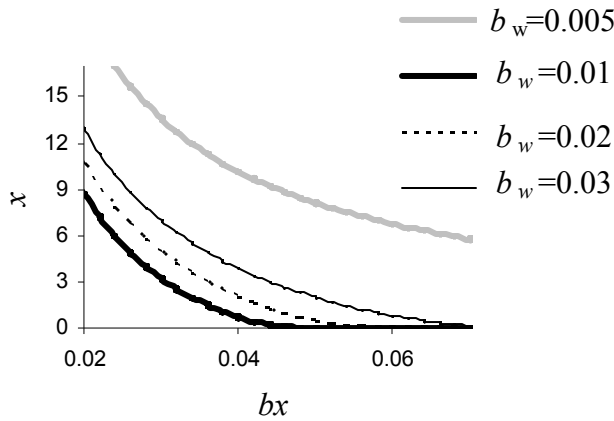


Figure 4.4: The relationship between attack coefficient of herbivores in the natural environment ( $b_x$ ) and the equilibrium density of wild host plant ( $x$ ) for different herbivores attack coefficients ( $b_w$ ) in the managed compartment.

Fig. 4.5 summarizes the combined effect of  $b_w$  and  $b_x$  on the desired species by indicating which parameter combinations enable survival and which ones lead to extinction of  $x$ . The lowest values of  $b_x$  at which extinction occurs, are for  $b_w = 0.01$ , where the spillover effect is maximal. For lower  $b_w$ , the spillover effect rapidly dissipates, and hence much greater attack rates  $b_x$  are needed to drive  $x$  to extinction. If  $b_w$  is set to 0 (i.e. no spillover) extinction occurs only at a  $b_x$  of 3.83 ( $(\text{shoot}/\text{m}^2)^{-1} \text{ yr}^{-1}$ ). Likewise, the spillover effect is reduced when  $b_w$  increases beyond 0.01, and accordingly, higher attack rates  $b_x$  are required to exterminate  $x$  at increasing  $b_w$ .

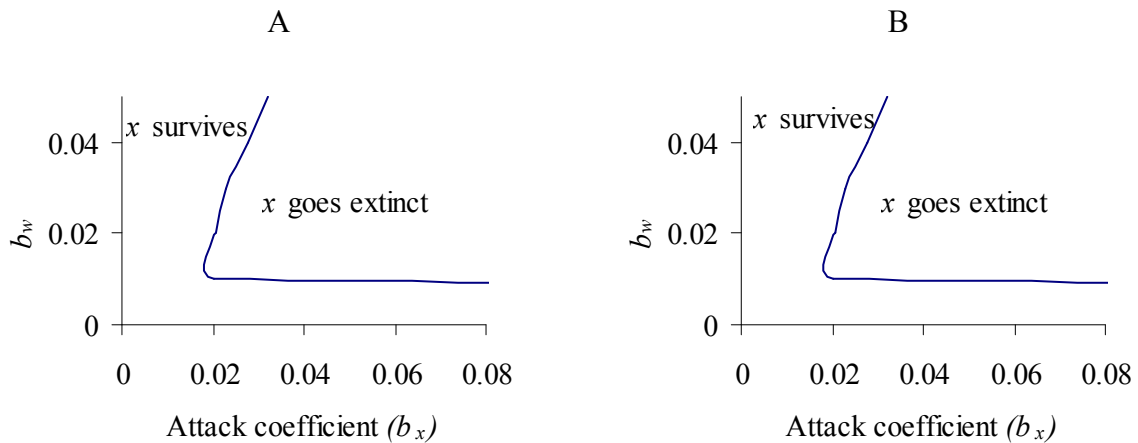


Fig. 4.5: Extinction threshold of wild host plant ( $x$ ) determined by both the herbivore's attack coefficient in the managed compartment ( $b_w$ ) and in the natural ecosystem ( $b_x$ ).

(A): dispersal coefficient is 0.5;

(B): dispersal coefficient is 2.5.

Other parameter values are set at their default values. Note when the density of wild host plant is lower than  $0.1 \text{ shoot}/\text{m}^2$  it is regarded as extinct.

The dispersal coefficient mediates the spillover effect that is responsible for the effect of the enemy-weed interaction in the managed compartment on the extinction of  $x$  in the natural compartment. For high dispersal rate (Fig. 4.5B), the area of extinction of  $x$  is much larger than for a low dispersal rate (Fig. 4.5A). The threshold between the area of extinction and survival shows transition from equilibrium  $\mathbf{xiv}$  to  $\mathbf{x}$  (Table 4.2).

The fundamental effect of the dispersal parameter,  $d$ , is to equilibrate the densities of the natural enemy in the managed and natural compartments. If  $d$  is large, any differences are equilibrated very quickly, while, if  $d$  is small, some difference may be maintained between the enemy densities in the two compartments, due to differences in production and loss rates of enemies in the two compartments. There is more herbivore production in the managed compartment because the resident population of the weed is bigger than that of the species  $x$  in the natural compartment, so an increase in  $d$ , *decreases* enemy density in the managed compartment and *increases* density in the natural compartment due to increased spillover. As a result of the resulting decrease in  $x$  at greater spillover,  $y$  is released and its density increased (Fig. 4.6).

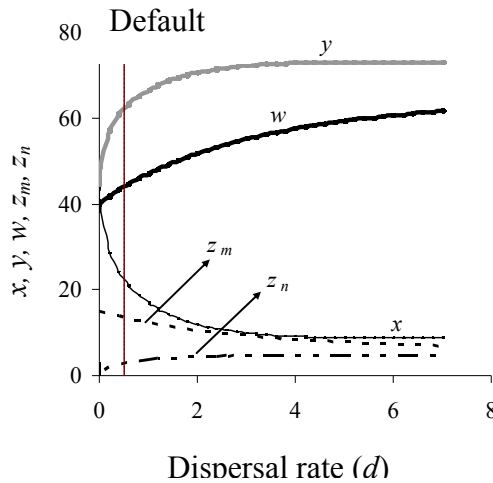


Fig. 4.6: The relationship between dispersal rate  $d$  of the herbivore and the equilibrium densities of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed compartment ( $z_m$ ), herbivores in the natural compartment ( $z_n$ ), weed ( $w$ ). Vertical line present the default values for  $d$ , other parameter values are set at their default.

As shown in Fig. 4.7, the results of combined parameter changes are predictable from the above reported effects of changes in single parameters. For instance, when the competitiveness of the competing species in the natural compartment is enhanced by increasing  $a_{xy}$  from 0.8 to 0.95, then over a wide range of attack coefficients,  $b_x$  and  $b_w$ , the density of the desired species  $x$  is diminished (Fig. 4.7A). Likewise, enhancing the spillover effect by increasing the dispersal coefficient  $d$ , diminishes the density of the desired species

over a wide range of attack rates,  $b_x$  and  $b_w$  (Fig. 4.7B). Increasing the death rate of the enemy enhances densities of species  $x$  (Fig. 4.7C). Herbivores with a low death rate can drive the wild host plant to extinction, even if their attack rates ( $b_x, b_w$ ) are low.

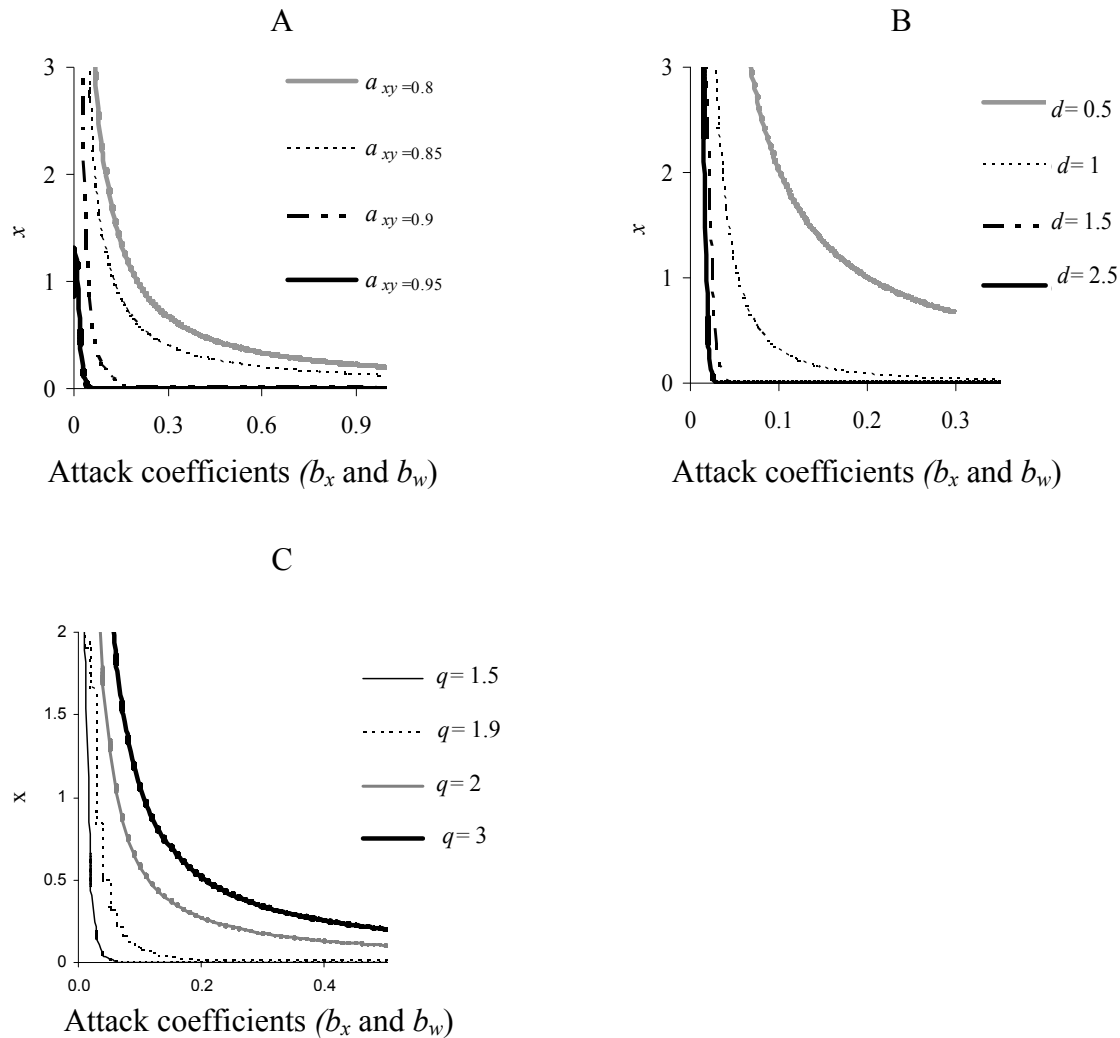


Fig. 4.7: The relationship between attack coefficients  $b_w$  and  $b_x$  of the herbivore and the equilibrium density of species  $x$  for different levels of (A)  $a_{xy}$  (B) dispersal coefficient (C) herbivore's death rate  $q$ . Vertical line present the default values for  $b_x$  and  $b_w$ , and other parameter values are set at their default.

## 4.5 Discussion

This paper puts forward a theoretical model framework for analysing which factors contribute to extinction risk of a wild non-target plant species due to spillover of a natural enemy introduced for biological control in agriculture. Extinction is enhanced by: (1) a large resident population of the natural enemy in the agriculture compartment, which is the case at intermediate values of the attack rate on the target weed; (2) a high attack rate of the enemy on the non-target wild species; (3) a high dispersal rate of the herbivore between the managed (target) compartment and the natural (non-target) compartment; and (4) presence in the

natural compartment of a competitor species with high degree of niche overlap with the non-target host.

We highlight the importance of competition between plant species for the extinction of the wild host plant. Wild plant species which have a strong competitor are highly vulnerable to a mild attack from herbivores whereas wild plant species that do not have a strong competitor are better able to survive under attack from an introduced herbivore. Therefore, before introducing a herbivore, land managers have to study competition pressure on potential non-target host plants of the natural enemy considered for introduction. If a potential non-target host plant species is under high competitive pressure from other plants, the introduction of the herbivore to the managed compartment should be considered risky.

We showed that the dispersal quantity of the herbivore species plays an important role in the extinction of the favourable wild host plant species. Rand et al. (2006) suggested that spillover may negatively affect the natural habitat, but recommends further studies to clarify to what extent spillover of a natural enemy can influence the natural habitat. We show that spillover cannot only reduce the density of plant species in the natural habitat but also can cause extinction of a wild species. We demonstrated that the risk of extinction can be higher when the herbivores have a low attack rate on the targeted plant species due to high abundance of their host plants. This is in contrast with conclusions so far in the literature. Because a higher herbivore attack rate results in a lower density of their host plant species (Begon et al. 1996), herbivores with a lower attack rate have been regarded as safer for wild plant species. This also means that herbivores with lower attack rate on the target plants are not only doing a poor job in reducing the density of targeted plants (e.g. weeds) but also can pose a larger risk to wild species in the natural habitat.

#### 4.6 Conclusions

We have analyzed how the introduction of a herbivore as a biological control agent in a managed compartment such as an agricultural system can cause biodiversity loss in the natural system by its spillover effects. We distinguished a two compartments model system: 1) a managed compartment where locally a herbivore ( $z_m$ ) is introduced to control a pest weed ( $w$ ), and 2) a nature compartment where the same herbivore species (here denoted as  $z_n$ ) can attack a wild plant species. It is possible that the herbivore establishes itself and affects wild plant species in the natural compartment. The risk of reducing biodiversity is highest if the dispersal rate of the herbivores between natural and managed compartment is high, and if the host plant in the natural compartment is under strong competition with other plant species. Therefore, the introduction of the herbivores when the conditions of the site allow for a high dispersal of herbivores from the managed compartment can result in biodiversity loss in the natural area. It is crucial that before introducing a biological control agent, the managers monitor the natural area for wild or protected plant species that can be on the menu of the

proposed agent. If a wild plant species in the natural habitat is attacked by herbivores and is already under high competition pressure from other plants, even with a low herbivores dispersal, wild plant species can go extinct. We also conclude that the spillover of herbivores from a managed to a natural environment can cause extinction of a wild plant species, even if some parameter values suggest a low risk. Herbivores with a lower attack rate can reach high population densities in the managed compartment. In this case herbivores can highly disperse to the natural habitat and put a wild plant species at the risk of extinction. Therefore, our recommendation to land managers is to be very cautious with the introduction of herbivores with a low attack rate for the target plant species.

### **Acknowledgments**

We thank Arjan Ruijs for his direction at the initial stage of developing this chapter.

#### A4.1 Appendix

##### Non-dimensionalization

In order to facilitate mathematical analysis with respect to finding the equilibria and their stability by reducing the number of parameters, the system of five model equations is first

non-dimensionalized by setting  $t = \frac{T}{d}$ ,  $x = k_x X$ ,  $y = k_y Y$ ,  $z_n = \frac{d}{b_x}$ ,  $z_m = \frac{d}{b_w}$ ,  $w = k_w W$ . We get:

$$\left. \begin{aligned} \frac{dX}{dT} &= \alpha X(1 - X - \beta Y) - Z_n X \\ \frac{dY}{dT} &= \gamma Y(1 - Y - \delta X) \\ \frac{dZ_n}{dT} &= \vartheta X Z_n - \zeta Z_n + \left(\frac{1}{\eta} Z_m - Z_n\right) \\ \frac{dZ_m}{dT} &= \varepsilon W Z_m - \zeta Z_m + (\eta Z_n - Z_m) \\ \frac{dW}{dT} &= \mu W(1 - W) - W Z_m \end{aligned} \right\} \quad (\text{A4.1})$$

Where  $X$  is the non-dimensionalized density of the non-target species,  $Y$  is the non-dimensionalized density of its wild competitor,  $W$  is the non-dimensionalized density of weeds in the agriculture compartment,  $Z_m$  is the non-dimensionalized density of herbivores in the managed compartment, and  $Z_n$  is the non-dimensionalized density of herbivores in the natural compartment. The non-dimensional parameters are defined as:

$$\alpha = \frac{r_x}{d}, \beta = \frac{a_{xy} k_y}{k_x}, \gamma = \frac{r_y}{d}, \delta = \frac{a_{yx} k_x}{k_y}, \varepsilon = \frac{f}{d} b_w k_w, \zeta = \frac{q}{d}, \eta = \frac{b_w}{b_x}, \vartheta = \frac{f}{d} b_x k_x, \mu = \frac{r_w}{d}.$$

##### Derivation of the equilibria

From system (A4.1) we get the following conditions that have to be combined for getting the equilibria

$$(\text{Ia}) X = 0 \vee (\text{Ib}) Z_n = \alpha(1 - X - \beta Y)$$

$$(\text{IIa}) Y = 0 \vee (\text{IIb}) Y = 1 - \delta X$$

$$(\text{III}) Z_n - \vartheta X Z_n + \zeta Z_n = \frac{1}{\eta} Z_m$$

$$(\text{IV}) Z_m - \varepsilon W Z_m + \zeta Z_m = \eta Z_n$$

$$(\text{Va}) W = 0 \vee (\text{Vb}) \mu(1 - W) = Z_m$$

The combination of conditions (III) and (IV) give either no insects present or the insects present in both compartments. No extra equilibria are found for the combinations (Ia, IIa, Va

and insects present) and (Ia, IIb, Va and insects present) because of internal inconsistency. A summary of the results is given in Table 4.2.

### Stability analysis of steady states

The general Jacobian Matrix in equilibrium point  $(\bar{X}, \bar{Y}, \bar{Z}_n, \bar{Z}_m, \bar{W})$  is:

$Jac(general) =$

$$\begin{pmatrix} \alpha(1-2\bar{X}-\beta\bar{Y})-\bar{Z}_n & -\alpha\beta\bar{X} & -\bar{X} & 0 & 0 \\ -\gamma\delta\bar{Y} & \gamma(1-2\bar{Y}-\delta\bar{X}) & 0 & 0 & 0 \\ g\bar{Z}_n & 0 & g\bar{X}-\zeta-1 & \frac{1}{\eta} & 0 \\ 0 & 0 & \eta & \varepsilon\bar{W}-\zeta-1 & \varepsilon\bar{Z}_m \\ 0 & 0 & 0 & -\bar{W} & \mu(1-2\bar{W})-\bar{Z}_m \end{pmatrix}$$

To test the stability of each equilibrium we substitute the equilibrium densities of all 5 interaction state variables and parameter values in the Jacobian matrix. If all 5 generated eigenvalues have negative real parts the equilibrium is (locally) stable. Otherwise the equilibrium is unstable. Analytical analysis show that equilibria (I-VI) are unstable (saddle points). For the other steady states a numerical analysis has been performed.



## Invasive species: economic analysis of dispersal, plant competition and herbivory

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**ABSTRACT**

Introducing natural enemies (herbivores) to control for invasive plant species on agricultural land can be a cost effective way of increasing agricultural productivity. This, however, can pose external costs to nature if the herbivore spills over to nature and targets indigenous species. We investigate how to control for these herbivores that spill over to nature, while attacking indigenous species that compete with other, non-attacked plants. A bio-economic modelling approach is used to find optimal management strategies for the parameter space for which indigenous plants have a high risk of extinction and for parameters that play an important role on the economics of control. We show that herbivores that have a higher attack rate on non-target species need more control. Paradoxically, species with a *lower* attack rate on the target species also need *more* control. Optimal control levels are higher when the non-targeted host species in nature have a higher value than their competitors, or if costs of control are lower. If the non-target species gets a low density due to competition with other plants and herbivory the level of control is high as well. It has also been shown that more control is needed if the dispersal rate of herbivores is moderately low.

**Keywords**

Invasive species, Externality, Economics, Dispersal, Plant competition, Herbivory

## 5.1 Introduction

It has been documented that agricultural activities have resulted in a reduction of biodiversity and degradation of the ecosystem (e.g. Stanners and Bourdeau 1995; Bigna 1998). Even though many farmers have been successful in increasing food production in the 20<sup>th</sup> century, remarkable achievements in the agricultural lands also imposed costly environmental problems (Conway and Pretty, 1991; Pretty 1998; Krebs et al. 1999; Pretty et al. 2000). In Germany for example, total external costs of modern agriculture are estimated to be \$81-117/ha for arable land and pastures (only for pesticides and gaseous emissions), \$112-274/ha for arable land in USA and approximately \$370/ha for arable land and pastures in the UK (Pretty et al. 2000 and 2001). One of the agricultural activities that can cause negative external effects on nature is the control of weed by introducing biological control agents. The use of biological agents as natural enemies of weed is widely regarded as a cost effective, safe and suitable means for controlling invasive species (Ehler 1998; Thomas and Willis 1998; Pemberton 2000). These biological agents, however, can pose environmental risks to indigenous plant species (Thomas and Willis 1998; Follett and Duan 1999; Wajnberg et al. 2001). For example in Northern America, a biological control herbivore that was introduced to control invasive Pitcher's thistle (*Cirsium pitcheri*), also attacked Platte thistle (*Cirsium canescens*) which is a valuable protected thistle (Louda et al. 2003; Louda et al. 2005). Many of the biological agents introduced for invasion control on agricultural lands can feed on alternative hosts in natural habitats and may disperse between agricultural and natural systems (Symondson et al. 2002; Rand et al. 2006; Wirth et al. 2007). These biological agents can produce large negative effects in the natural habitats by their spillover or cross-edge invasion effects (Suarez et al. 1998; Cronin et al. 2005; Rand et al. 2006). Spillover of an insect herbivore, which is a biological agent to control weed, from managed land (e.g. agricultural land) to natural land (e.g. a meadow) can reduce biodiversity. Therefore, the spilled over herbivore acts as an invasive species in the natural land where it causes economic losses. Control of such an invasion is inevitable as it may cause considerable damage (Östman et al. 2003; Hougner et al. 2006).

There is a considerable body of literature on the economics of invasion control strategies (e.g. insects) in agriculture (see e.g. Carlson and Wetzstein (1993); Brown et al. (2002); Chalak-Haghighi et al. (2008a, and b)). This literature mostly deals with the effectiveness of control and the feasibility of control strategies on reducing invasion on agricultural land. Carlson et al. (1989), for instance, studied the economic returns of controlling the cotton boll weevil in California. Many studies investigate timing, and optimal treatment of insect herbivore invasions (Regev et al. 1976; Onstad et al. 2002; Crowder 2005; Dasgupta et al. 2006). In order to assess the optimal strategy to control for the herbivore that spilled over from agricultural (managed) land, ecological impacts and their interactions with other species

on agriculture and natural land need to be understood in more detail. Because ecological and economic conditions of the managed and natural systems can differ, interaction between different plant species within the ecological system (e.g. competition) and their economic values can result in different optimal control strategies. Herbivores can disperse fast or slowly between the systems, which can affect the dynamics of species in both systems and consequently alters economic output of managed and natural land.

The few studies on such spillovers are recent, and focus mainly on the ecological side of the spillover effect (see Rand et al. 2006). Still, economic analysis on control strategies for herbivore spillover from managed to natural land (due to the externality of weed management) that can threaten biodiversity, deserves more attention.

The control level is affected both by economic and ecological conditions. Ecological interactions are very complex and the details of species competition or cooperation processes are affected by many unknown or unexpected relations, which make economic analysis and the finding of optimal control measures difficult. Despite the complexity of the ecological-economic system, it is important to gain understanding of these processes, using a bio-economic model which accounts for the main structure of the ecological-economic dynamics of such an externality.

This study puts forward a novel bioeconomic analysis to find the optimal control strategies. We study the control of a herbivore which attacks an invasive species on agricultural land, but which also disperses to the natural land where it affects competitive processes of indigenous plant species. This allows us to evaluate the interaction between control for this herbivore, processes of competition, herbivory (i.e. consumption of plants by the herbivore) and dispersal which can avoid or reduce unfavourable, unexpected or even catastrophic shifts in natural ecosystems. In addition to that, it allows us to derive control strategies for which the benefits obtained from the managed land and from nature are maximized. We perform a sensitivity analysis with our bio-economic model, in order to explore the relationship between optimal levels of control and the key parameters. We assume that a herbivore that is introduced to a managed compartment to control for weed invasion, can disperse and cause externalities in a natural compartment. In the natural compartment the herbivore can cause damages to a wild host species, and therefore has to be controlled for. The optimal control is high when the density of wild non-target host species is low due to factors such as high competition pressure from other species, or high damage by herbivory.

## 5.2 Description of the bioeconomic model system

We construct a bio-economic model to control for a non-indigenous herbivore in nature. This herbivore has been introduced to agricultural land to control for weed, but disperses to nature where it causes externalities. To analyze the interaction between control strategies,

competition, herbivory and dispersal we distinguish two parts in our bio-economic model: 1) a managed compartment (e.g. agricultural land) in which a herbivore ( $z_m$ ) is introduced to control a pest weed ( $w$ ) in order to increase agricultural benefits, and 2) a natural compartment (e.g. an unmanaged ecosystem) to which the same herbivore species (here denoted as  $z_n$ ) can disperse and attack a wild plant species (Fig. 5.1) which causes negative externalities. In the latter compartment, species interaction is exemplified by considering two competing plant species. The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment, herbivores attack a non-target host plant species ( $x$ ) which competes with another plant species or group of species ( $y$ ). This causes economic losses and poses negative external effects. The main focus in the bio-economic model are herbivory, competition, dispersal and

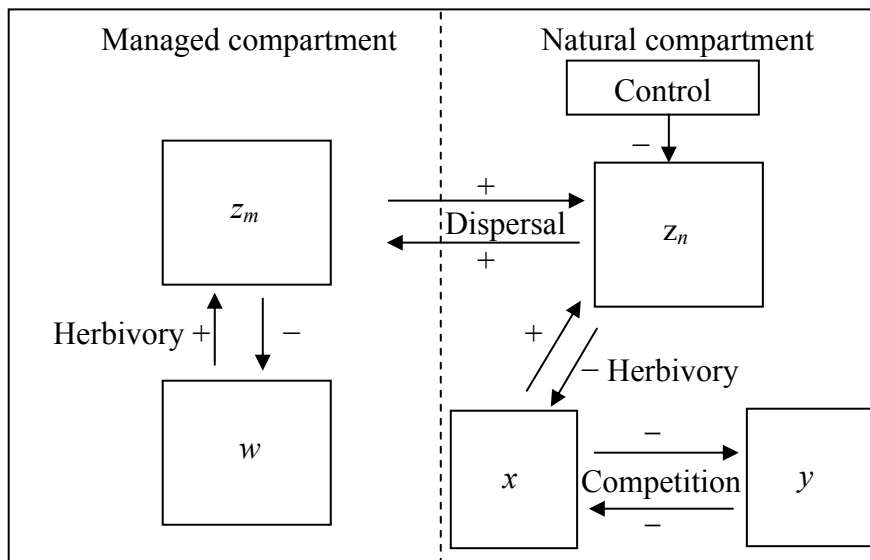


Fig. 5.1: Schematic representation of the bio-economic system. Note that the introduction of a herbivore in the managed compartment (e.g. pasture) suppresses the weed population. Herbivores disperse to the natural compartment and feed on an endemic plant species ( $x$ ), which is in competition with (an) other plant species ( $y$ ). Species  $z_m$  represents the population of the herbivore in the managed compartment and  $z_n$  represents the population of the same herbivore species in the natural compartment. Control reduces the density of herbivores in the natural compartment and releases wild host plant ( $x$ ) from herbivory.

Without the insect herbivore, the two compartments (Fig. 5.1) would be strictly separated: the weed in the managed compartment would not influence the coexisting competing plant species in the natural compartment. If herbivores did not disperse they would generate benefits in the managed compartment by controlling weed but would not have a negative effect on the natural compartment. However after introduction of herbivore and in the presence of dispersal, the two compartments are linked. The link between species  $w$  (the weed) and  $x$  (the non-target wild species) can be characterized as apparent competition which means that they share a common predator (Holt 1977). It is assumed that the initial situation

in the natural compartment is characterized by a stable equilibrium, i.e. individuals of each of the competing species have less competitive effect on the other species than on their own; they have sufficient niche differentiation to enable coexistence (Begon et al. 1996).

The arrival of a herbivore in the natural compartment, which is assumed to attack one of the competing species, *viz*  $x$ , can offset the initially stable equilibrium between  $x$  and  $y$ , by reducing the density of plant species  $x$ . The competing plant species  $y$  can benefit, resulting in an increase in its density, while the non target host plant,  $x$ , might go extinct due to the combination of herbivory and competition. The suppressive effect of herbivores on the wild non-target species can be further aggravated by sustained spillover of the herbivore from the managed compartment. In the natural compartment herbivore can be controlled, in order to increase density of  $x$  and reduce the negative externality.

Control and dispersal of the herbivore influences herbivore densities and that of its host plant species ( $x$  and  $w$ ) in both compartments. Net dispersal of herbivores is assumed to be density dependent and always towards the compartment with a lower density\*. As the managed compartment can carry high population of weed, it can produce a large population of herbivores and cause substantial herbivore spillover to the natural compartment.

In the full system, complex interactions exist between control and species. A mathematical analysis and numerical exploration and sensitivity analysis of a bio-economic model are used to elucidate these interactions. Below, we first describe in more detail the set up of the different elements of the bio-economic model.

### 5.2.1 Ecological system

The dynamics of the weed density,  $w$ , is modelled with a logistic growth function:

$$\frac{dw}{dt} = wr_w \left( 1 - \frac{w}{k_w} \right) \quad (5.1)$$

Where parameter  $r_w$  is the growth rate of the weed ( $\text{yr}^{-1}$ ), and parameter  $k_w$  represents the carrying capacity of the land for weed ( $\text{m}^{-2}$ ). All model parameters are listed in Table 5.1. The dynamics of the weed after introduction of the herbivore and with a density  $z_m$  ( $\text{m}^{-2}$ ) changes into:

$$\frac{dw}{dt} = wr_w \left( 1 - \frac{w}{k_w} \right) - b_w z_m w \quad (5.2)$$

where parameter  $b_w$  represents the attack rate or the rate that one individual of species  $z_m$  successfully encounters one shoot of weed per unit of time (year).

The competitive interaction between plant species  $x$  and  $y$  in the natural compartment is modelled as a standard Lotka-Volterra system (e.g. Begon et al. 1996):

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\* We assumed that insects move randomly and towards the compartment with lower density which is the simplest assumption (see Kareiva 1983). This facilitates our complex mathematical analysis.

$$\begin{cases} \frac{dx}{dt} = r_x x \left( 1 - \left( \frac{x + y a_{xy}}{k_x} \right) \right) \\ \frac{dy}{dt} = r_y y \left( 1 - \left( \frac{y + x a_{yx}}{k_y} \right) \right) \end{cases} \quad (5.3)$$

where variables  $x$  and  $y$  represent the density of the two competing species. Parameters for carrying capacities are denoted as  $k_x$  and  $k_y$ , and for their intrinsic growth rates as  $r_x$  and  $r_y$ . The per capita competition effect of species  $y$  on species  $x$  is represented by parameters  $a_{xy}$ . Parameter  $a_{yx}$  denotes the reciprocal effect.

After the herbivore has reached the natural compartment, the Lotka-Volterra competition model changes into:

$$\begin{cases} \frac{dx}{dt} = r_x x \left( 1 - \left( \frac{x + y a_{xy}}{k_x} \right) \right) - b_x z_n x \\ \frac{dy}{dt} = r_y y \left( 1 - \left( \frac{y + x a_{yx}}{k_y} \right) \right) \end{cases} \quad (5.4)$$

where variable  $z_n$  represents the density of herbivores in the natural compartment, parameter  $b_x$  represents the attack rate or rate that one individual of species  $z_n$  successfully encounters one shoot of species  $x$  per unit of time (year).

The dynamics of the herbivore in both the managed and the natural compartment is modelled as a Lotka-Volterra equation for predators. If metapopulation dynamics are also included, this can be represented as:

$$\begin{cases} \frac{dz_n}{dt} = f b_x x z_n - q z_n - g z_n + d (z_m - z_n) \\ \frac{dz_m}{dt} = f b_w w z_m - q z_m + d (z_n - z_m) \end{cases} \quad (5.5)$$

where variables  $z_m$  and  $z_n$ , respectively represent the densities of herbivores in the managed and natural compartment, parameter  $g$  is a control measure to reduce the herbivore population in the natural compartment, parameter  $d$  is the dispersal rate of herbivores between the two compartments, parameter  $f$  (fecundity coefficient) measures the number of herbivores that can be produced by reducing one shoot of their host plant. The term  $f b_x x z_n$  represents the herbivores birth rate in the natural compartment and parameter  $q$  represents their mortality rate.

We analyse the 5-dimensional system comprising the 2 plant species equations (5.4), the two herbivore equations (5.5) and the weed equation (5.2), in an effort to understand the possible equilibrium solutions and their stability. We first look at the ecological system without considering control, i.e. assuming that  $g=0$  in (5.5). Non-dimensionalization of the system (see appendix 4.1) reduces the number of parameters from 13 (Table 4.2) to nine. This

eases solving the model and moreover, the definition of new parameters, based on combinations of the original parameters, helps us to see which changes in original parameter values have more or less the same effect on equilibrium values and/or stability.

There exist at least 14 biologically relevant equilibria for the non-dimensionalized system which are listed in Table 4.2. In the second part of the appendix 4.1 we derive the conditions to obtain equilibria. The combinations of these conditions provide a number of equilibria that are also given in Table 4.2. Equilibrium **i**, where all state variables are zero, is trivial. There are three equilibria with a single non-zero state variable (**ii**, **iii** and **iv**), three equilibria with 2 non-zero state variables (equilibria **v**, **vi** and **vii**), 3 equilibria with 3 non-zero state variables (**viii**, **ix**, and **xi**), and 3 equilibria with 4 non-zero state variables (**x**, **xii**, and **xiii**). There is a single equilibrium in which all 5 species can coexist (**xiv**). It should be noted however, that, depending on the parameter values, equilibrium **xiv** can also result in a biologically irrelevant equilibrium solutions, i.e. with negative densities.

We are interested in the stable equilibria of the system. To have a locally stable equilibrium (attractor), all eigenvalues of the Jacobian matrix for that equilibrium should be negative. When an equilibrium is unstable, a small movement away from the equilibrium increases its distance from the equilibrium in the course of time. This can eventually lead to extinction of one or more species. For all equilibria, except equilibria (**i-vi**) derivation of the eigenvalue signs is not possible, even though we simplified the model by non-dimensionalization. Thus, we were not able to get explicit expressions for the stability of the different equilibria. For that reason, we performed a numerical analysis, which shows that most equilibria are unstable for a wide range of parameter values. From an application point of view, the first six equilibria (equilibria **i-vi** in Table 4.2), which have no herbivores, are irrelevant. After all, we introduced the herbivores assuming that they would establish. Only two equilibria are of particular interest: 1) an equilibrium in which all species coexist (a positive solution for equilibrium **xiv**), and 2) an equilibrium in which species *x* goes extinct because of the herbivores attack (equilibrium **x**).

### 5.2.2 The economic system

Benefits are generated from two parts of the system: the managed compartment and the natural compartment. The benefits obtained from the managed compartment depend on the number of shoots of endemic plants in the managed compartment. They are calculated as follows:

$$B = F(1 - w/k_w) \quad (5.6)$$

where parameter  $F$  represents the benefits obtained from the managed compartment in the absence of weed. In the absence of weed, the number of endemic species reach their carrying capacity and benefits are at their maximum level. When weeds invade, they replace the endemic plant in the managed compartment and reduce benefits.



In the natural compartment, we assume that benefits, which may be intangible, are function of the densities of species  $x$  and  $y$ . These benefits are assumed to follow a Cobb-Douglas function.<sup>†</sup> Therefore the benefit of the whole ecosystem will be calculated from the following:

$$V(x, y, w, g) = \mu x^\rho y^\varphi - cg + B \quad (5.7)$$

where  $\rho$  and  $\varphi$  are strictly positive parameters and  $\rho + \varphi = 1$ .  $\mu$  is a parameter to convert the species density to a monetary value. Parameter  $g$  represents the level of control for the herbivore (equation 5.5) and can be defined as exponential decay of herbivores caused by control effort (e.g. by applying insecticides). Parameter  $c$  represents the costs of herbivore control per control unit (e.g. insecticides) and  $B$  measures the net benefit obtained from the managed compartment (see (5.7)).

A manager chooses for the level of herbivore control that maximizes the discounted present value of the benefit function subject to the ecological dynamics of the species (equation 5.2, 5.4, and 5.5). Therefore, we have the following optimal control problem:

$$\max_g \int_0^\infty V(x, y, w, g) e^{-\sigma t} dt \quad (5.8)$$

subject to (5.2), (5.4), and (5.5), where  $\sigma$  represents the discount rate.

For the above optimization problem the present value Hamiltonian is:

$$\begin{aligned} H = & \mu x^\rho y^\varphi - cg + F(1 - w/k_w) + \Upsilon \left\{ r_x x \left( 1 - \left( \frac{x + a_{xy}y}{k_x} \right) \right) - b_x z_n x \right\} + \Theta \left\{ r_y y \left( 1 - \left( \frac{y + a_{yx}x}{k_y} \right) \right) \right\} \\ & + \Xi \left\{ fb_w w z_m - q z_m + d(z_n - z_m) \right\} + \Psi \left\{ fb_x x z_n - q z_n - g z_n + d(z_m - z_n) \right\} + \xi \left\{ wr_w \left( 1 - \frac{w}{k_w} \right) - b_w z_m w \right\} \end{aligned} \quad (5.9)$$

The first-order optimality conditions are:

$$\frac{\partial H}{\partial g} = -\psi z_n - c = 0 \quad (5.10)$$

$$\dot{x} = \frac{\partial H}{\partial \Upsilon} = r_x x \left( 1 - \left( \frac{x + a_{xy}y}{k_x} \right) \right) - b_x z_n x \quad (5.11)$$

$$\dot{y} = \frac{\partial H}{\partial \Theta} = r_y y \left( 1 - \left( \frac{y + a_{yx}x}{k_y} \right) \right) \quad (5.12)$$

$$\dot{z}_m = \frac{\partial H}{\partial \Xi} = fb_w w z_m - q z_m + d(z_n - z_m) \quad (5.13)$$

<sup>†</sup> It is acknowledged that there may be a host of different functions translating species densities in the nature compartment, or translating biodiversity levels, into a monetary value. Analysis of the effect of alternative functional forms is kept for future research.

$$\dot{z}_n = \frac{\partial H}{\partial \Psi} = fb_x x z_n - q z_n - g z_n + d(z_m - z_n) \quad (5.14)$$

$$\dot{w} = \frac{\partial H}{\partial \xi} = r_w w \left(1 - \frac{w}{k_w}\right) - b_w z_m w \quad (5.15)$$

$$\begin{aligned} \dot{\Upsilon} = \sigma \Upsilon - \frac{\partial H}{\partial x} = \sigma \Upsilon + \Upsilon \left( \frac{r_x x}{\kappa_x} - r_x \left( 1 - \left( \frac{x + a_{xy} y}{k_x} \right) \right) + b_x z_n \right) + \frac{\alpha_{yx} r_y \Theta y}{\kappa_y} \\ - \rho \mu y^\rho x^{\rho-1} - b_x f \psi z_n \end{aligned} \quad (5.16)$$

$$\dot{\Theta} = \sigma \Theta - \frac{\partial H}{\partial y} = \sigma \Theta - r_y \Theta \left( 1 - \left( \frac{y + a_{yx} x}{k_y} \right) \right) + \frac{r_y \Theta y}{k_y} + \frac{\alpha_{xy} r_x \Upsilon x}{k_x} - \phi \mu x^\rho y^{\rho-1} \quad (5.17)$$

$$\dot{\Xi} = \sigma \Xi - \frac{\partial H}{\partial z_m} = \sigma \Xi - \Xi(b_w f w - d - q) + b_w \xi w - d \Psi \quad (5.18)$$

$$\dot{\Psi} = \sigma \Psi - \frac{\partial H}{\partial z_n} = \sigma \Psi - d \Xi + b_x \Upsilon x - \Psi(b_x f x - d - q - g) \quad (5.19)$$

$$\dot{\xi} = \sigma \xi - \frac{\partial H}{\partial w} = r \xi - \xi \left( r_w \left( 1 - \frac{w}{k_w} \right) - b_w z_m - \frac{r_w w}{k_w} \right) + \frac{F}{k_w} - b_w f z_m \Xi \quad (5.20)$$

where  $\Upsilon, \Theta, \Xi, \Psi$  and  $\xi$  are multipliers of  $x, y, z_m, z_n$  and  $w$ , respectively which can be interpreted as the shadow prices for the respective equations.

For a locally stable equilibrium (attractor), five of the eigenvalues of the Jacobian matrix for that equilibrium should be negative. Analysis shows that if the Jacobian matrix of only the ecological part indicates that the equilibrium is unstable, then the full bio-economic system (i.e. including the economic constraints) is also unstable. For instance, for the equilibria of the bio-economic model that are conform equilibrium **i-vi** (see Table 4.2), both the Jacobian matrices of only the ecological system and the Jacobian matrix of the bio-economic system indicate that the equilibrium is unstable. Due to the complexity of the model, for the other equilibria, the interpretation of the derivation of the sign of all eigenvalues is not possible analytically, even though we simplified the model by non-dimensionalization. In the remainder of this paper, we therefore, use a numerical analysis to explore the characteristics of the equilibria.

### 5.3 Numerical analysis

As noted above, from an application point of view, two equilibria are of particular interest: 1) an equilibrium in which all species coexist and 2) an equilibrium in which species  $x$  goes extinct because of the herbivore attacks. A trajectory that is of particular interest is one that starts when the herbivore is still not introduced and which is close to a positive equilibrium, which then moves towards an equilibrium without species  $x$  when the herbivore is introduced. This trajectory would allow us to observe the relationship between the optimal control

strategy and species densities for parameter values which can force plant species  $x$  to extinction. In the model, species  $x$  can reach a stable steady state where it gets a zero or negative growth after introduction of the herbivores, because  $x$  is suppressed by two forces : 1) competition with  $y$ , and 2) herbivory.

Below, we explore the parameter space and provide figures that can describe the relationship between optimal control, species density and some of the parameter values. In these figures only stable equilibria are represented. The results of the sensitivity analysis are only given for a selection of parameters for which the results are not trivial. For the other parameters, their effects on the optimal level of control and on species densities can be derived from the analysis in the appendix 4.1 (on the non-dimensionalisation). For example, the effects of  $k_x$  and  $k_y$  can be deduced from the illustrated effects of  $a_{yx}$  and  $a_{xy}$ . As shown in the appendix 4.1, the ratio  $k_y/k_x$  has the same fundamental influence on system dynamics as  $a_{xy}$ , while the ratio  $k_x/k_y$  has the same fundamental influence on system dynamics as  $a_{yx}$ .

Parameter values for the numerical illustration of the behaviour of the system are based on expert estimation (W. van der Werf and L. Hemerik personal communication) and literature data. They represent loosely a system of thistle species with a weevil species as herbivore (Table 5.1). All three species ( $x$ ,  $y$ , and  $w$ ) have a relative growth rate ( $r$ ) of  $0.3 \text{ yr}^{-1}$  and a carrying capacity ( $k$ ) of  $80 \text{ shoots m}^{-2}$  (Chalak-Haghighi et al. (2008a and b); Schwinning and Parsons 1999).

The attack coefficient of the herbivore species on the weed, ( $b_w$ ) and the wild species ( $b_x$ ) are  $0.01 (\text{shoot/m}^2)^{-1} \text{ yr}^{-1}$ . Competitive coefficients of both species ( $a_{xy}$  and  $a_{yx}$ ) are taken to be 0.8, representing a situation in which the species have rather similar resource requirements and niche overlap. The fecundity coefficient of the herbivore ( $f$ ) is 10 herbivores per shoot, and its death rate ( $q$ ) is  $4 \text{ yr}^{-1}$ . Finally, the dispersal coefficient ( $d$ ) is  $0.5 \text{ yr}^{-1}$ . Parameters  $\rho$  and  $\varphi$  represent the economic weight of  $x$  and  $y$  on the benefit function, and are set at 0.5. Costs per unit of control ( $c$ ) are set as an example at  $\text{€}0.01/\text{m}^2$ .  $\mu$  is assumed to be 1 at default and benefit obtained from a weed free pasture ( $F$ ) is set at  $\text{€}0.04/\text{m}^2$  (FADN 2004).

Table 5.1. An overview of default parameter values

Parameter	Unit	Default Value	Explanation
$r_x$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $x$ .
$k_x$	$\text{shoot}/\text{m}^2$	80	Carrying capacity of plant species $x$
$a_{xy}$	None	0.8	Competition coefficient of species $y$ with respect to species $x$ .
$b_x$	$(\text{shoot}/\text{m}^2)^{-1} \text{yr}^{-1}$	0.01	Attack rate of the herbivore $z$ on plant species $x$
$r_y$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $y$ .
$k_y$	$\text{shoot}/\text{m}^2$	80	Carrying capacity of plant species $y$
$a_{yx}$	None	0.8	Competition coefficient of species $x$ with respect to species $y$ .
$r_w$	$\text{yr}^{-1}$	0.3	Intrinsic growth rate of plant species $w$ .
$k_w$	$\text{shoot}/\text{m}^2$	80	Carrying capacity of plant species $w$
$b_w$	$(\text{shoot}/\text{m}^2)^{-1} \text{yr}^{-1}$	0.01	Attack rate of the herbivore $z$ on plant species $w$
$f$	$z \text{ shoot}^{-1}$	10	Fecundity coefficient of the herbivore
$q$	$\text{yr}^{-1}$	4	Relative death rate of the herbivore.
$d$	$\text{yr}^{-1}$	0.5	Dispersal coefficient of the herbivore
$c$	Euros	0.01	Control costs
$\rho$	None	0.5	Parameter value for species $x$
$\varphi$	None	0.5	Parameter value for species $y$
$g$	$\text{yr}^{-1}$	None	Control measure
$F$	Euros( $m^{-2} \text{yr}^{-1}$ )	0.04	Benefit obtained from the managed compartment in the absence of weed
$\sigma$	$\text{yr}^{-1}$	0.05	Discount rate
$\mu$	Euros	1	Converter of species density to monetary value

In the remainder of this section, we report the results of a sensitivity analysis to illustrate the relationship between optimal control, species densities and changes on the key parameters. In particular the parameters that have a considerable effect on spillover are considered. First, the effect of the competitive coefficient of  $y$  on  $x$ ,  $a_{xy}$ , is illustrated. Optimal levels of control increase as  $a_{xy}$  increases, until the moment when species  $x$  goes extinct (Fig. 5.2A).

As long as species  $x$  exists, for higher levels of  $a_{xy}$ , the marginal benefits of control increase due to which control levels also increase. Because of the assumed Cobb-Douglas functional form and the default parameter values adopted, the highest benefit from the nature compartment might be expected when species  $x$  and  $y$  have equal densities. We observe, however, a somewhat surprising result here. Fig. 5.2A. shows that even when the density of species  $x$  is higher than that of species  $y$ , it is still optimal to control for the herbivore and increase the density of  $x$ . The main reason for this is that the increase in the density of species  $x$ , due to control of herbivore, is higher than the decrease in the density of species  $y$ .

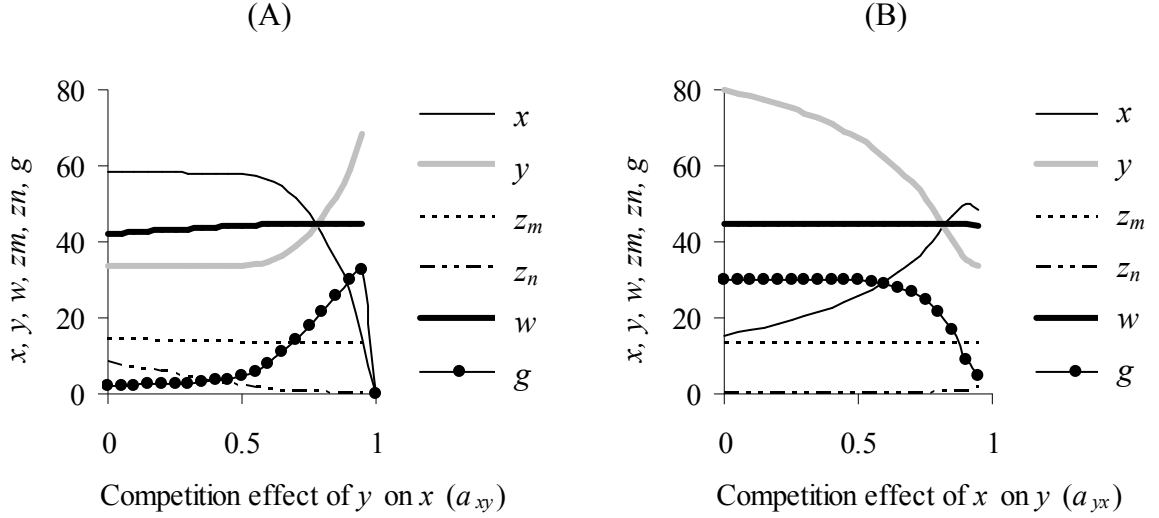


Fig. 5.2: The relationship between the optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and (A) competition effect of species  $y$  on  $x$  ( $a_{xy}$ ) (B) competition effect of  $x$  on  $y$  ( $a_{yx}$ ).

The reaction of species  $x$ , to a change in  $a_{xy}$ , is interesting. In the absence of control it is expected that an increase of  $a_{xy}$  will result in a decrease in species  $x$ . In the presence of control, however, and as long as  $a_{xy}$  is below a certain threshold level, the density of  $x$  does not change if  $a_{xy}$  increases. It decreases sharply, however, once the threshold level has been surpassed. The main reason is that, before the threshold level, the negative effect of  $a_{xy}$  on  $x$  is compensated by the positive effect of herbivore control on species  $x$ . If  $a_{xy}$  exceeds the threshold level, the negative effect of competition on  $x$  becomes so large that even very high herbivore control cannot compensate damages to the species  $x$ . Eventually, for large enough values of  $a_{xy}$ , species  $x$  goes extinct. When control increases as a response to the increase in  $a_{xy}$ , the equilibrium density of herbivores in the natural compartment goes down, as was expected. It hardly affects the managed compartment, however, because in the managed compartment the density of herbivores is maintained by feeding on the weed. The increased control reduces the density of herbivores in the natural compartment and causes a slightly higher spillover to the natural compartment and consequently a slight decrease of the herbivore density in the managed compartment. This slightly releases weed from the pressure of herbivory, increasing the density of weed.

Next, if the competitive effect of the desirable wild species  $x$  ( $a_{yx}$ ) increases, it is expected that  $x$  increases and  $y$  decreases. For low levels of  $a_{yx}$ , the herbivore is highly controlled for. The reason is that a low level of control would result in high herbivore densities, resulting in a very low density of  $x$ . Again, control is at a level that makes the marginal benefits of control equal to its marginal costs. For higher levels of  $a_{yx}$ ,  $x$  increases and reaches such a level that it does not pay off to keep herbivore densities at such a low level. Therefore, for higher levels of  $a_{yx}$ , a lower control level makes marginal costs and benefits of control equal. When  $a_{yx}$  increases, the equilibrium density of  $x$  goes up, while that

of  $y$  goes down because  $y$  gets released from competition with  $x$ . This is conform to the usual results from Lotka-Volterra competition models (Begon et al. 1996). For a large range of  $a_{yx}$ , the herbivores in the natural compartment are suppressed and kept constant by control, therefore their density is not responsive to an increase in the density of  $x$ . This constant level of herbivores also keeps the spillover and the density of herbivores in the managed compartment constant, resulting in unchanged density of weed. Only at very high levels of  $a_{yx}$  where control is low and  $x$  is high, the density of herbivores increases in the natural compartment. This increase of herbivores in the natural compartment reduces the spillover of herbivores from the managed compartment that leads to increasing herbivory pressure on the weed in the managed compartment therefore reducing, slightly, its density.

Secondly, the relationship between the attack coefficient  $b_x$  and control is straightforward (see equation 5.5 and Fig. 5.3). If this coefficient goes up, the birth rate of herbivore increases due to which herbivore densities will increase if there is no control. This would result in lower levels of  $x$  and consequently lower benefits. Herbivore control may increase benefits. Control will increase the density of  $x$  by reducing the density of the herbivore up to the point where the marginal costs and benefits of control are the same. As  $b_x$  increases, densities of species  $x$  go down, and consequently marginal benefits of control increase. Therefore to reach the economic optimum, herbivore control increases as  $b_x$  increases.

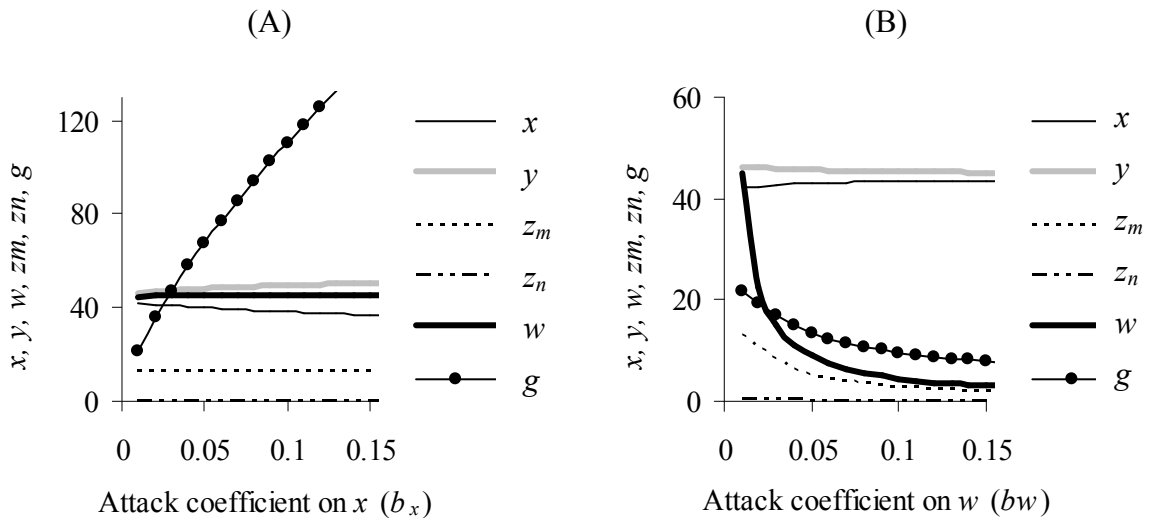


Fig. 5.3: The relationship between the optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and (A) herbivore attack coefficient on weed ( $b_x$ ), (B) herbivore attack coefficient on wild host plant ( $b_w$ ).

Results show that control keeps the level of herbivores in the natural compartment very low and constant. Fig. 5.3A shows that even a very high level of control can not entirely remove the herbivores from the natural compartment because of its spillover from the managed compartment. As  $b_x$  increases, its positive effect on herbivore density becomes slightly larger than the negative effect of control on herbivores. Thus the density of  $x$

decreases slightly, releasing  $y$  from competition with  $x$ , therefore increasing its density. However, an increase in  $b_x$  does not have a large effect on spillover of herbivores and weed density as the change in the density of herbivores in the natural compartment is very small.

Next, a change in  $b_w$  has a different effect on optimal control and species density than a change in  $b_x$  (see Fig. 5.3B). If this attack coefficient ( $b_w$ ) goes up, the weed density decreases. If the food source for herbivores (i.e. weed) decreases, herbivore densities decreases in the managed compartment. A lower density of herbivores in the managed compartment results in a lower spillover of herbivores to the natural compartment. Consequently attack on species  $x$  decreases. This reduces the marginal benefit of increasing the number of wild host plant due to the control. Therefore the optimal level of control goes down. As the spillover of herbivores to the natural compartment decreases, the density of species  $x$  increases slightly. Thus competition pressure on  $y$  increases and its density reduces slightly.

Third, the effect of the fecundity coefficient ( $f$ ) is straightforward (see Fig. 5.4). If this coefficient increases, the herbivores birth rate increases and the herbivore density in the managed compartment increases as well. As with increasing  $b_x$  levels, in the natural compartment, the density of herbivores is kept very low by choosing high levels of control in order to reduce economic damages on  $x$ . Therefore an increase in  $f$  is compensated by higher levels of control and densities of  $x$  and  $y$  remains relatively constant.

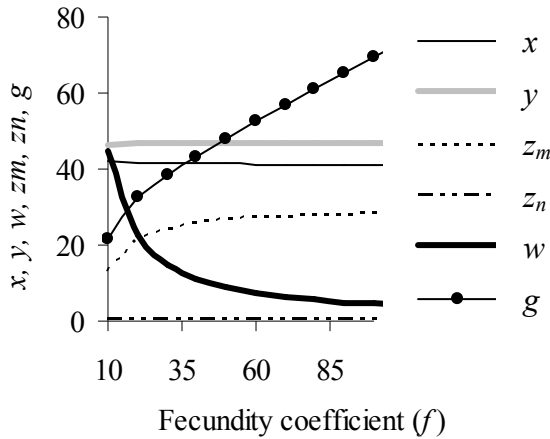


Fig. 5.4: The relationship between the optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and fecundity coefficient ( $f$ ).

Fourth, we consider the effect of the dispersal rate ( $d$ ). Note that species  $x$  has a lower density than  $w$ . This is because  $x$  highly competes with  $y$  (having default parameter values in Table 5.1). While, weed does not have such a competitor. Therefore herbivores have a larger source of food in the managed compartment, their density becomes larger in the managed

compartment. Thus if the dispersal coefficient ( $d$ ) increases, more herbivores spill over to the natural compartment, releasing weed from the pressure of herbivory due to which weed densities increase in the managed compartment. This results in increasing herbivory on  $x$  due to which its density decreases in the natural compartment. It releases  $y$  from competition with  $x$ , due to which its density increases (see Fig. 5.5).

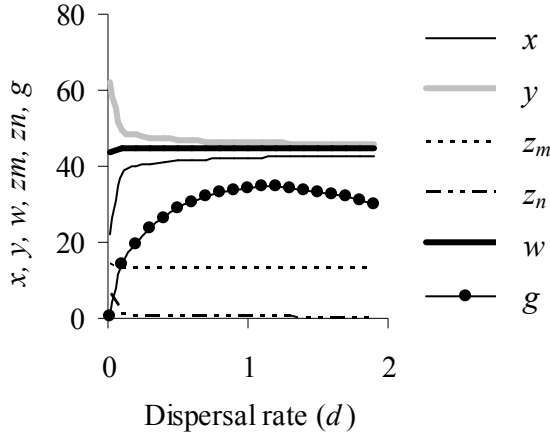


Fig. 5.5: The relationship between the optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and dispersal rate ( $d$ ).

This mechanism continues up to a threshold. After the threshold, the dispersal of herbivore between the two compartments is so high that the positive effect of control on  $x$  becomes higher than the negative effect of dispersal. The positive effect of control on the benefit is due to reducing herbivore density and increasing the density of  $x$ . Control negatively affects the benefit in the managed compartment, because control increases the spillover of herbivores from the managed to the natural compartment through reducing herbivore density in the natural compartment. This reduces herbivore density in the managed compartment, releasing weed from herbivory and increasing the density of weed. For a low level of the dispersal rate and up to a threshold, if the dispersal coefficient increases, the benefit of control to the natural compartment due to the increase in  $x$  becomes larger than the costs of control to the managed compartment due to the increase in weed. This occurs, because control only reduces the density of herbivores in the managed compartment through low dispersal. However, after the threshold and for high level of  $d$ , both compartments are much more interconnected. Therefore, herbivore control has a stronger effect on the weed density in the managed compartment. In other words, as the herbivore dispersal rate increases, the costs to the managed compartment of higher levels of control become larger than the benefits to the natural compartment due to protection of  $x$ . Therefore, for high levels of  $d$ , and after the threshold, the marginal costs and benefits are equal even at lower levels of control than before the threshold and when  $d$  is lower.



Fifth, the effect of scale parameter for benefit in the natural compartment ( $\mu$ ) on the optimal control and species densities is presented in Fig. 5.6. For low levels of  $\mu$ , the economic value of species  $x$  and  $y$  in the natural compartment is low. Therefore the optimal strategy is to have no or little control because marginal benefits of additional control are low. As a result, herbivore densities become higher in the natural compartment, resulting in low levels of  $x$  and consequently high levels of  $y$  released from competition. When  $\mu$  increases, marginal benefits of control become larger than marginal costs of control. Therefore, control increases at optimal. This decreases herbivory pressure on  $x$ , increasing the densities of  $x$  and increasing competition pressure on  $y$  due to which its density decreases. Moreover, a decrease in the herbivore density in the natural compartment, increases herbivore spillover from the managed to the natural compartment. As a result, herbivore densities in the managed compartment decrease. Thus weed density increases.

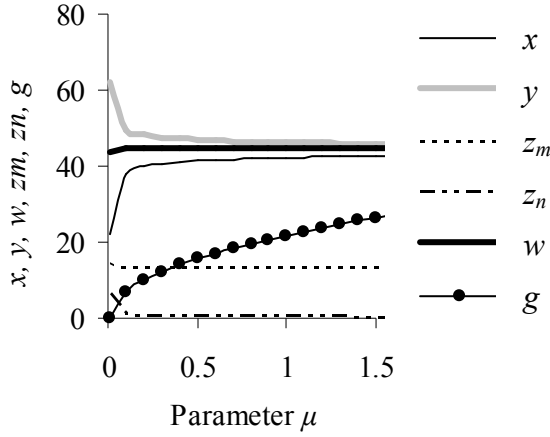


Fig. 5.6: The relationship between the optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and parameter  $\mu$ .

Sixth, the effect of  $\rho$ , on the optimal level of control is presented in Fig. 5.7. For low levels of  $\rho$ , the economic value of  $x$  is low as compared to that of  $y$ , therefore the optimal strategy is to have no or little control because marginal benefits of additional control are low. As a result, herbivore densities increase in the natural compartment, resulting in low  $x$  and consequently high levels of  $y$  released from competition. When  $\rho$  increases, species  $x$  becomes more important and marginal benefits of control increase. As a result, control levels increase, resulting in higher levels of  $x$ . This, suppresses herbivores in the natural compartment and increases  $x$  released from herbivory. Therefore, due to increased competition pressure on  $y$ , its density decreases. A decrease in the herbivore density in the natural compartment increases herbivore spillover to the natural compartment, thus reducing herbivore density in the managed compartment. As a result, the weed density increases.

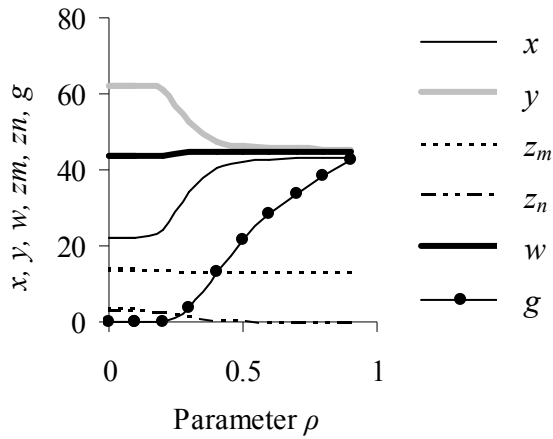


Fig. 5.7: The relationship between optimal control ( $g$ ), the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and parameter  $\rho$ .

Finally, the effect of control costs on the optimal strategy and species densities is presented in Fig. 5.8. If the control costs increase, the optimal level of control decreases. For very high control costs, optimal control even approaches zero. For higher marginal control costs, control levels will be adapted in such a way that marginal benefits of control equal its marginal costs. This is reached at lower equilibrium level of  $x$ . If control declines, herbivore densities in the natural compartment increase.

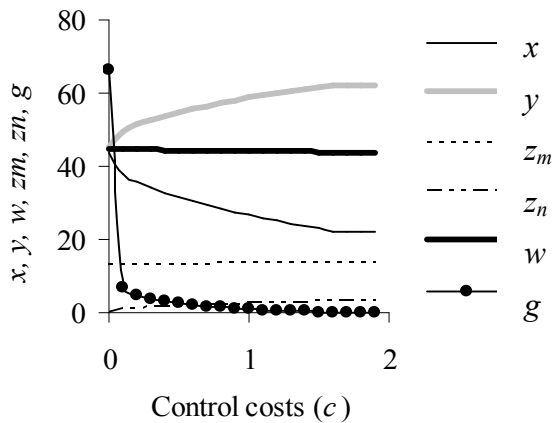


Fig. 5.8: The relationship between optimal control, the equilibrium density of wild host plant ( $x$ ), its competitor ( $y$ ), herbivores in the managed and natural compartments ( $z_m$  and  $z_n$ ), weed ( $w$ ), and costs of control ( $c$ ).

This increases herbivory pressure on  $x$ , decreasing densities of  $x$  and releasing  $y$  from competition due to which its density increases. Moreover, an increase in the herbivore density

in the natural compartment, decreases herbivore spillover from the managed to the natural compartment. As a result, herbivore densities in the managed compartment marginally increase, slightly reducing the weed density.

## 5.4 Conclusions

This paper analyses strategies for controlling a situation in which a herbivore that is introduced in a managed land (i.e. managed compartment) to control weed, spills over to a natural habitat (i.e. natural compartment) where it targets a wild species. A bioeconomic model has been set up and a numerical analysis has been performed in order to analyse the relationship between control levels, competition, herbivory, dispersal and a number of key parameters.

A herbivore that is introduced to a managed compartment to control weed, can disperse to a natural compartment and attack a non-target wild plant species. Thus herbivores may cause externalities in the natural compartment which need to be controlled. The results of the analysis show that the optimal level of control is high when the density of the wild, non-target host species is low. We also conclude that herbivores that have a higher attack rate on weed may need a lower control. The main reason for this is that herbivores with a higher attack rate on weed, produce a lower population in the managed compartment, due to which there is a lower spillover to the natural compartment. Next, for the attack rate of herbivores on non-target wild species, we show that its effect on optimal control is different. The higher this attack rate the higher the control level needed. Furthermore, we find an ambiguous relationship between dispersal rate of herbivores and optimal control. When the dispersal rate is low, an increase in the dispersal rate increases the level of control and when the dispersal rate is high an increase in the dispersal rate, decreases the level of control. Economic values of a non-target host plant and its competitor(s) highly influence the optimal level of control. When the non-target host species has low value as compared to its competing species, a low control would be needed to suppress herbivores. We recommend environmental managers to control for externalities that introducing a herbivore can cause to a natural compartment due to attack on a non-target wild plant species. This is especially so if the non-target species has a low density due to high competition with other plant species, heavy attack by herbivores or high herbivores spillover.

Although the benefits of the introduction of biological control agents depend on the specific local ecological and economic circumstances, our analysis illustrates that severe risks exist that biological control agents have a negative impact on ecosystems. This calls for a very strict assessment and screening on the relevant criteria before biological control agents are newly introduced. In many cases it will be very difficult to control the agents, once they have established in natural systems, and the required control costs could be well in excess of the benefits of the biological control agent that were initially expected. For future research,

we recommend more complex production function and utility functions be analyzed. We also suggest studying the interaction of more complex species in the natural system, since non-linear interactions may results in counter-intuitive results, as was shown in our analysis.

### **Acknowledgments**

We are grateful to Dr. Lia Hemerik for her support to the stability analysis and suggestions for parameter values in the ecological model. We also express our gratitude to Dr. Wopke van der Werf for his comments on the parameter values.

## Discussion and conclusions

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## 6.1 Introduction

This thesis had two main aims. The first aim is to analyse the control of an invasive plant in an agricultural system. As a case study I use the Californian thistle in New Zealand, in order to assist farmers in New Zealand to find the most cost effective strategies for controlling Californian thistle in their pastures. In order to do so, I applied a systematic analysis that used new modelling elements and in this way I contributed to the literature on invasive species control. The second aim of this thesis was to study the negative externalities that controlling invasion in agriculture can pose to ecosystems. To achieve the first aim, both deterministic and stochastic dynamic programming models were set up to find cost effective methods to tackle the problem of Californian thistle. For the second aim, I set up an ecological and a bio-economic model in which species interactions were analysed in an ecosystem consisting of two compartments with dispersal of the natural enemy between an agricultural and a natural compartment. The structure of this chapter is as follows. Section 6.2 presents the answer to research questions posed in Chapter 1. In Section 6.3 conclusions are drawn with respect to the appropriateness and set up of the models used and the policy implications. Finally, in Section 6.4 suggestions for future research are presented.

## 6.2 Answers to the research questions

In this section, the answers to the different research questions as dealt with in the different chapters of this thesis, will be discussed.

*Q1. What is the best modelling approach to tackle the problem of Californian thistle and what are the most cost effective strategies to control it? (Chapter 2)*

To answer this question, a deterministic dynamic programming approach was followed in order to analyse management of pastures that are infested with Californian thistle in New Zealand. It has been shown that the optimal Integrated Weed Management (IWM) strategy is to apply a combination of control options even for low densities of Californian thistle. The analysis showed that the introduction of an insect herbivore (*Apion onopordi*) as biological control agent results in increase in net present value (NPV) by maximally 2 percent. This implies that the insect can be excluded from the control option at a cost lower than 2 percent of the NPV, and this would be the opportunity costs of avoiding the ecological risks related to its release. The analysis shows that a combination of introduction of the insect, intensified grazing and MCPA are optimal at lower levels of the thistle density. For higher thistle densities, it is optimal to also include mowing in January and mycoherbicides. Next to that, I also showed that excluding herbicides from the control option reduces NPV maximally by 2

percent. Therefore, herbicides can be replaced by more environmentally friendly options at costs lower than 2 percent of the NPV.

*Q2. How to model the problem of Californian thistle when some control options have stochastic effects and which are the best control options under a stochastic setting? (Chapter 3)*

Establishment of a biological agent highly depends on the environmental conditions due to which the effect of biological control on invasive species is stochastic. For that reason, I set up a stochastic dynamic programming model, in which the effects of two biological control agents (i.e. the insect and mycoherbicides) on the invasive species are stochastic.

For the model setting and parameter space adopted, results showed that despite of the stochastic efficacy of the two biological control agents, it is still optimal to introduce them to the pastures in New Zealand assuming they have no adverse effect on other species. Including stochasticity of the impact of the insect does not affect the optimal strategy adopted. The main reason for this result is that the insect can be introduced at relatively low costs and that it will remain active once it is introduced. However, the analysis showed that in case of stochasticity, mycoherbicides will only be adopted at higher thistle densities. This means that if stochasticity would not have been considered, farmers would introduce mycoherbicides already in an earlier state.

The analysis indicates that when chemicals (i.e. MCPA and MCPB) are included in the list of control options, for most ranges of thistle densities (densities between 17 and 61 shoot/m<sup>2</sup>) the best IWM strategies are to apply MCPA, overgrazing and introduction of the insect. If chemicals are excluded, for most densities, the optimal IWM strategy also includes use of mycoherbicide and mowing in January and March. Excluding chemicals and using more environmentally friendly options can be done at the maximum cost of 1.3 percent of NPV.

*Q3. How can a biological control agent that is introduced to reduce the invasive species in an agricultural system affect the risk of extinction of a wild plant species? (Chapter 4)*

An ecological model has been set up in which two separate compartments are distinguished: 1) a managed compartment (i.e. agricultural land) where a herbivore (i.e. biological agent) is introduced to control an invasive plant (i.e. weed), and 2) a natural compartment (e.g. non-managed system) where the same herbivore species can attack a wild desirable plant species. The two herbivore populations are linked by dispersal, enabling the herbivore to spill over

from one compartment to the other. In the natural compartment herbivores attack a non-target host plant species which competes with another plant species or group of species. The main processes in the model are herbivory, competition and dispersal.

Results show how the introduction of a herbivore as a biological control agent to reduce weed invasion in a managed compartment can cause biodiversity loss in a natural compartment due to spillover effects. It is possible that the herbivore establishes itself and even puts wild species in the natural compartment at the risk of extinction. The risk of reducing biodiversity is highest if the dispersal rate of the herbivores between natural and managed compartment is high, and if the host plant in the natural compartment is under strong competition with other plant species. Therefore, the introduction of herbivores, when site conditions allow for high dispersal rates, can result in biodiversity loss in the natural area. An interesting phenomenon is the existence of a nonlinear relationship between the number of herbivores and weed density. If the attack coefficient of herbivores in the managed compartment increases, herbivore densities increase up to a point where the weed density becomes very low due to herbivory, due to which herbivores densities go down again. If the attack coefficient of herbivores is becoming large enough to enable a significant population of herbivores, the weed density decreases. This means that a moderate attack coefficient in the managed compartment can produce high herbivores densities and generate high spillover effects. It can also be concluded that spillover of herbivores from a managed to a natural compartment can cause extinction of a wild plant species, even if some parameters values such as the attack coefficient on weed suggest a low risk.

*Q4. What is the best option from an economic point of view to protect a wild plant species if it suffers from attack by a herbivore which disperses from and to the agricultural land? (Chapter 5)*

A bioeconomic model has been set up in which, as discussed above, two compartments are distinguished. The compartments, species interactions and dispersal are similar to the ecological model used to answer the third research question. To answer the fourth research question, however, a control measure has been introduced that reduces the herbivore density in the natural compartment due to which the wild plant species is protected from herbivory. This enables understanding the relationship between the most cost effective control levels and key ecological and economic parameter values. Here cost-effectiveness, not only considers economic benefits from agriculture but also intangible benefits from maintenance of biodiversity.

I showed that if the non-targeted host plant receives a *higher* competition pressure from its plant competitors in the natural land, the marginal revenues of control *increase* and consequently the control level *increases*. If the attack coefficient of herbivores on the non-



target host plant goes up, the birth rate of herbivore increases. Therefore, without control it is expected that the herbivore density increases. This would result in lower density of wild host species and consequently lower benefits. Here, herbivore control may increase benefits. The control increases the density of the wild host plant through reducing the density of herbivores, up to the optimal level where the marginal costs and benefits of control become equal. If the attack coefficient on the host wild species increases, the density of wild host plant goes down, and consequently marginal benefits of control become larger. To reach the equilibrium, in case of increasing attack coefficients, herbivore control has to increase. The optimal control, however, responds differently to changes in the herbivore attack coefficient on the invasive plant. If this attack coefficient goes up, the weed density decreases. If the food source for herbivores (i.e. weed) decreases, herbivore densities decrease in the managed compartment. A lower density of herbivores in the managed compartment results in a lower spillover of herbivores to the natural compartment. Consequently attack on species  $x$  decreases. This reduces the marginal benefit of increasing the number of wild host plant due to the control. Therefore the optimal level of control goes down. Furthermore, it has also been shown that optimal levels of control chosen depend largely on the values of the economic parameters. For instance, a much larger control level is needed if the economic value of the wild species that is targeted by herbivores is high. After all, in that case, the marginal benefits of increasing the number of wild host plants by control become larger.

### 6.3 Conclusions

#### *Methodology*

In this study, I combined ecological and economic knowledge in a bio-economic framework to analyse the adverse effects of invasive species on the ecosystem and to find the most cost-effective IWM strategies to control them. For each research question analysed, a different methodology had been adopted in order to be able to analyse the system in the best possible way.

Some studies focus on the benefit-cost ratios of control strategies in a static framework (e.g. Headley 1985; CRC 2001; McConnachie et al. 2003). These studies have not fully captured the dynamic processes which have been shown to be very important in this thesis. In that respect, a dynamic programming approach is much more suitable. Several studies also used a dynamic programming method, like e.g. Bulte and van Kooten (1999), Wu (2001), Odom et al. (2003) and Jones et al. (2006). In this thesis, I make a contribution to the literature by performing a dynamic programming analysis in which two different categories of control strategies are considered, each with different dynamics. The first category concerns

control strategies that have to be selected on an annual basis. The second category is a once-and-for-all choice, meaning that once applied they will not have to be repeated in the future.

Next, I develop a stochastic dynamic optimisation model to analyse whether including stochastic effects of biological control changes the optimal control strategies adopted. There have been comparable studies in the literature, like e.g. Pandey and Medd (1991), Higgins et al. (1997), and Cacho et al. (2008). This thesis, however, makes new contributions to the methodologies applied previously. Firstly, I conduct a stochastic optimisation model with a discrete decision variable consisting of the 62 feasible combinations of integrated control strategies as mentioned above. In the existing literature, either a single or only a few continuous decision variables were analysed. In reality, however, the question is often not which level of a single control strategy to adopt, but which combination of feasible control options is most efficient. Secondly, a complication of the stochastic model set up here is that some control options have to be chosen on an annual basis, whereas others (for example, the introduction of the weevil) have to be introduced only once, after which it will remain active.

Furthermore, I analysed whether the introduction of a biological control agent in a managed compartment can cause a spillover effect that causes extinction of a wild endemic species in a natural compartment. Previous studies showed that introducing a biological agent in a managed compartment can pose spillover effects on a natural compartment (e.g. Rand et al. 2006). I, however, make a new contribution to this literature by introducing a novel modelling approach to analyse the conditions under which the dispersal of a biological control agent from a managed to a natural system results in a spillover effect, threatening biodiversity. In the model, two compartments are distinguished: a managed compartment where locally a herbivore is introduced to control a weed, and a natural compartment where the same herbivore species can attack a wild plant species, in that way affecting the dynamics between different species. The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment, herbivores attack a non-target host plant species which competes with another plant species or group of species. The main processes in the model are herbivory, competition and dispersal.

Finally, cost-effectiveness of controlling herbivores in the natural compartment is analysed. Related studies focussing on similar economic questions include e.g. Carlson and Wetzstein (1993) and Brown et al. (2002). This thesis, however, makes a new contribution by finding the optimal level of control in a system which takes into account competition, herbivory, dispersal and control, for a two compartment system as described above.

## Policy

In this thesis, I studied IWM strategies consisting of 62 control strategies for controlling Californian thistle. Some authors argued that biological control is a more suitable and cost effective means of controlling invasive plants (e.g. Hill and Greathead 2000; Pemberton 2000). In this thesis, however, it has been shown that excluding the insect from control options reduces the net present value maximally by 2 percent. Some authors claim that intensified grazing is less effective and less attractive than other control methods (e.g. Popay and Field 1996). I, however, showed that intensified grazing is part of an integrated weed management strategy to deal with Californian thistle. Although this option can be less effective than other control options, its low costs make it an attractive control option to be used in combination with other control measures.

In this thesis, I conclude that eradication of Californian thistle is not possible with the available control strategies, while Olson et al. (2002) concluded that eradication is the optimal way of dealing with invasion. Because there are, so far, no control options that allow for total eradication of the thistle, Olson's conclusion remains rather theoretical. Moreover, I showed that excluding chemicals from control strategies, reduces the net present value maximally by 2 percent. This shows that replacing them with more environmentally friendly control options can be done at costs lower than 2 percent of the NPV. This contrasts with other studies (e.g. Benz et al. 1999), who encourage the use of chemicals because of their cost effectiveness.

Even though biological control, as compared to other control methods such as chemicals, is regarded as a safer and more suitable control option, they are not easily chosen, because of their low efficacy (Dixon et al. 1994; Reglinski et al. 1994; Lyon et al. 1995). I, however, concluded that a mycoherbicide (*Sclerotinia Sclerotiorum*) is an effective way of controlling thistle and a good replacement for chemicals.

Biological agents introduced to agriculture for reducing the negative effects of invasive species can spillover to nature and pose negative effects to it (Rand et al. 2006). The extent of these negative effects, however, has not been systematically analysed. This thesis puts forward a theoretical model framework for analysing which factors contribute to the extinction risks of a wild non-target plant species due to spillover of a herbivore introduced for biological control in agriculture. I concluded that extinction is enhanced by: (1) a large resident population of the herbivore in the agriculture compartment, which is the case at intermediate values of the attack rate on the target weed; (2) a high attack rate of the herbivore on the non-target wild species; (3) a high dispersal rate of the herbivore between the managed (target) compartment and the non-target (natural) compartment; and (4) presence in the natural compartment of a competitor species with high degree of niche overlap with the non-target host. This thesis highlights the importance of competition between plant species on the risk of extinction of the wild host plant. Wild plant species

which have a strong competitor are highly vulnerable to a mild attack from herbivores whereas wild plant species that do not have a strong competitor are better able to survive under attack from an introduced herbivore.

I showed that the number of herbivores that spill over plays an important role in the risk of extinction of the favourable wild host plant species. Rand et al. (2006) suggested that spillover may negatively affect the natural habitat, but recommended further studies to clarify to what extent spillover of a natural enemy can influence the natural habitat. This thesis showed that spillover cannot only reduce the density of plant species in the natural habitat but also cause extinction of a wild species. It has been demonstrated that the risk of extinction can be higher when the herbivores have a low attack rate on the targeted plant species due to high abundance of their host plants. This contrasts with conclusions that have been drawn in the literature so far. Because a higher herbivore attack rate results in a lower density of their host plant species (Begon et al. 1996), herbivores with a lower attack rate have been regarded as safer for wild plant species. This also means that herbivores with a lower attack rate on the target plants are not only doing a poor job in reducing the density of targeted plants (e.g. weeds) but also can pose a larger risk to wild species in the natural habitat.

Finally, an economic analysis is performed that finds the optimal control measure to deal with the externalities caused by spillover of a biological agent. Economic analyses focussing on the optimal control of biological agents, mostly consider effectiveness of control and the feasibility of control strategies in agricultural land (Carlson and Wetzstein 1993; Brown et al. 2002). This thesis, however, looks at the relationship between optimal control and three processes: 1) herbivory on two plant species in two separate compartments (i.e. weed in managed compartment and wild host plant in the natural compartment), 2) competition between host plant species and other plants in the natural compartment, and 3) dispersal of herbivores between the managed and the natural compartment.

For higher dispersal rates, a higher level of optimal control might be expected, but I showed that increases in the dispersal rate only increase the optimal control up to a threshold level. After this threshold level, higher dispersal rates result in lower optimal control. I also showed that if a herbivore is introduced with a low attack rate on the target plants, more control of the herbivore is needed to protect the wild plant. This result is counterintuitive, because so far, literature regards herbivores with lower attack rate as safer (Begon et al. 1996). Thus, one might at first sight expect that a herbivore with a lower attack rate would need lower control.

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## 6.4 Suggestions for future research

The analyses presented in this thesis offer useful frameworks for controlling invasive species problems. Below, I highlight some methodological aspects and policy issues that have not been addressed in this thesis but that demand for more in-depth analysis in future research.

### *Method*

This thesis introduced a set of control options for different level of weed densities on a yearly basis. It is recommended to use shorter time steps in order to be able to take into account seasonal changes of plant dynamics and control efficacy. This thesis employed a stochastic dynamic optimisation framework to deal with the stochastic efficacies of biological control agents. Even though less stochasticity can be expected from other control options such as chemicals and mechanical control, it would be interesting to analyse the interrelationships between the stochastic effects of a number of control options as well as of invasive plant dynamics.

In this thesis, I used a modelling approach to elucidate risks of introduction of a herbivore species for biological control of a weed in agriculture and analysed the optimal strategy to control it. The model includes key processes such as the interaction between a herbivore and its target and non-target species, dispersal of the enemy from one ecosystem compartment to another, and the competitive relationships between a non-target species with other species in a natural compartment. It also analysed the optimal strategy to control herbivores in the natural compartment. Beside the processes that are considered in this analysis, there can be numerous other processes, which go beyond the scope of this research but deserve to be addressed in future studies. These processes could include competition or predator-prey interaction of spilled over herbivores with other herbivores species. The dispersal of herbivores between the two compartment also can be modelled differently and based on the density of their host plants. It is also interesting to look at control methods that are able to limit the dispersal of herbivores between the two compartments.

### *Policy*

Invasive species have characteristics that can take advantage of global change. As compared to endemic species, there is evidence that they respond stronger to CO<sub>2</sub> concentration in the atmosphere and to nitrogen deposition. Increasing amounts of invasive species also provides feed back effects which can result in enhanced global change (see Dukes and Mooney 1999; Botkin et al. 2007). Therefore, I recommend to consider the relationship between global warming and the invasion of species and their control options. Finally, for controlling Californian thistle, it is suggested to initiate more studies on the efficacies of control

strategies when they are integrated with other control options and to use the synergetic effects of combined options. There is a lack of information on efficacy of IWM strategies and on the synergies that can be reached.

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Invasive species are one of the most significant threats to biodiversity and agricultural production systems. The majority of our natural ecosystems suffer from invasive species. Alien weeds are the most costly invasive species leading to huge worldwide economic damages. Production losses due to invasion and costs of controlling invasion generate large economic damages.

This thesis has two main aims. The first aim is to analyse the control of an invasive plant in an agricultural system. As a case study I use the Californian thistle in New Zealand, in order to assist farmers in New Zealand to find the most cost effective strategies for controlling Californian thistle in their pastures. With a systematic analysis that uses new modelling elements I contribute to the literature on invasive species control. The second aim of this thesis is to study the negative externalities that controlling invasion in agriculture can pose to ecosystems. To achieve the first aim, both deterministic and stochastic dynamic programming models are set up to find cost effective methods to tackle the problem of Californian thistle. For the second aim, I develop an ecological and a bioeconomic model for the agricultural system and the related natural system.

The case study focuses on New Zealand, which is a country with a very diverse and valuable natural resources base. Today New Zealand ranks among the highest invaded areas in the world. Many weeds impede pastoral farming in New Zealand and one of the most important of these is Californian thistle (*Cirsium arvense*). Californian thistle is a very troublesome weed because it is more difficult to control than other invasive plants and is called one of the world's worst weeds.

To achieve the broad aims of this research, Chapters 2-5 of this thesis answer several research questions.

Chapter 2 investigates the best modelling approach to tackle the problem of Californian thistle and studies the most cost effective strategies to control it. To tackle the problem of Californian thistle in New Zealand several control options are available. I consider integrated weed management strategies (IWM) that combines 4-chloro-2-methylphenoxy (MCPA), 4-(4-chloro-2-methylphenoxy) (MCPB), intensified grazing, mycoherbicides, mowing in January and mowing in March and introduction of the insect (*Apion Onopordi*). Combining these seven control options gives 62 feasible IWM strategies. A deterministic dynamic programming model is developed to study the most cost effective IWM strategies. I use a deterministic dynamic programming model that handles a large number of decision variables in two categories: reversible and irreversible. It has been shown that the optimal Integrated Weed Management (IWM) strategy is to apply a combination of control options even for low densities of Californian thistle. The analysis shows that the introduction of an insect herbivore (*Apion onopordi*) as biological control agent results in an increase in net present value (NPV) of maximally 2 percent. This implies that the insect can be excluded from the control option at a cost lower than 2 percent of the NPV, and this would

be the opportunity costs of avoiding the ecological risks related to its release. The analysis shows that a combination of introduction of the insect, intensified grazing and MCPA are optimal at lower levels of the thistle density. For higher thistle densities, it is optimal to also include mowing in January and mycoherbicides. In addition to that, I also show that excluding herbicides from the control option reduces NPV maximally by 2 percent. Therefore, herbicides can be replaced by more environmentally friendly options at costs lower than 2 percent of the NPV.

Chapter 3 models the problem of Californian thistle when biological control agents have stochastic effects on the thistle and analyses the best control options under a stochastic setting. For that reason, I set up a stochastic dynamic programming model, in which the effects of two biological control agents (i.e. the insect and mycoherbicides) on the invasive species are stochastic. For the model setting and parameter space adopted, results show that despite of the stochastic efficacy of the two biological control agents, it is still optimal to introduce them to the pastures in New Zealand assuming they have no adverse effect on other species. Including stochasticity of the impact of the insect does not affect the optimal strategy adopted. However, the analysis shows that in case of stochasticity, mycoherbicides will only be adopted at higher thistle densities. This means that if stochasticity would not have been considered, farmers would introduce mycoherbicides already at lower thistle densities. The analysis indicates that when chemicals (i.e. MCPA and MCPB) are included in the list of control options, for most ranges of thistle densities (densities between 17 and 61 shoot/m<sup>2</sup>) the best IWM strategies are to apply MCPA, overgrazing and introduction of the insect. If chemicals are excluded, for most densities, the optimal IWM strategy also includes use of mycoherbicide and mowing in January and March. Excluding chemicals and using more environmentally friendly options can be done at the maximum cost of 1.3 percent of NPV.

Chapter 4 studies the effect of introduction of a biological control agent that is introduced to reduce an invasive species in an agricultural system, on the risk of extinction of wild plant species. Biological agents such as insect herbivores (e.g. weevils) that help reducing the invasive species in agricultural systems may disperse to other parts of the ecosystem and target desirable species. I set up an ecological model in which two separate compartments are distinguished: 1) a managed compartment (i.e. agricultural land) where a herbivore (i.e. biological agent) is introduced to control an invasive plant (i.e. weed), and 2) a natural compartment (e.g. non-managed system) where the same herbivore species can attack a wild desirable plant species. The two herbivore populations are linked by dispersal, enabling the herbivore to spill over from one compartment to the other. In the natural compartment herbivores attack a non-target host plant species which competes with another plant species or group of species. The main processes in the model are herbivory, competition and dispersal. Results show it is possible that the herbivore establishes itself and even puts wild species in the natural compartment at the risk of extinction. The risk of reducing biodiversity is highest if the dispersal rate of the herbivores between natural and managed

compartment is high, and if the host plant in the natural compartment is under strong competition with other plant species. Therefore, the introduction of herbivores, when site conditions allow for high dispersal rates, can result in biodiversity loss in the natural area. An interesting phenomenon is the existence of a nonlinear relationship between the number of herbivores and weed density. If the attack coefficient of herbivores in the managed compartment increases, herbivore densities increase up to a point where the weed density becomes very low due to herbivory, due to which herbivores densities go down again. If the attack coefficient of herbivores is becoming large enough to enable a significant population of herbivores, the weed density decreases. This means that a moderate attack coefficient in the managed compartment can produce high herbivores densities and generate high spillover effects. I also concluded that the spillover of herbivores from a managed to a natural compartment can cause extinction of a wild plant species, even if some parameters values such as the attack coefficient on weed suggest a low risk.

Chapter 5 analyses the best option from an economic point of view to protect a wild plant species if it suffers from attack by a herbivore which disperses from and to the agricultural land. I set up a bioeconomic model in which, as discussed above, two compartments are distinguished. The compartments, species interactions and dispersal are similar to the ecological model used in Chapter 4. In this chapter, however, I introduce a control measure that reduces the herbivore density in the natural compartment due to which the wild plant species is protected from herbivory. This enables understanding the relationship between the most cost effective control levels and key ecological and economic parameter values. Here cost-effectiveness not only considers economic benefits from agriculture, but also intangible benefits from maintenance of biodiversity. I show that if the non-targeted host plant receives a *higher* competition pressure from its plant competitors in the natural compartment, the marginal revenues of control *increase* and consequently the control level *increases*. If the attack coefficient of herbivores on the non-target host plant goes up, the birth rate of herbivores increases. Therefore, without control it is expected that the herbivore density increases. This would result in lower density of wild host species and consequently lower benefits. Here, herbivore control may increase benefits. The control increases the density of the wild host plant through reducing the density of herbivores, up to the optimal level where the marginal costs and benefits of control become equal. If the attack coefficient on the host wild species increases, the density of wild host plant goes down, and consequently marginal benefits of control become larger. To reach the equilibrium, in case of increasing attack coefficients, herbivore control has to increase. The optimal control, however, responds differently to changes in the herbivore attack coefficient on the invasive plant. If this attack coefficient goes up, the weed density decreases. If the food source for herbivores (i.e. weed) decreases, herbivore densities decrease in the managed compartment. A lower density of herbivores in the managed compartment results in a lower spillover of herbivores to the natural compartment. As a consequence, attack on the wild host plant

decreases. This reduces the marginal benefit of increasing the number of wild host plant due to the control. Therefore the optimal level of control goes down. Furthermore, it has also been shown that optimal levels of control chosen depend largely on the values of the economic parameters. For instance, a much larger control level is needed if the economic value of the wild species that is targeted by herbivores is high. After all, in that case, the marginal benefits of increasing the number of wild host plants by control become larger.

Chapter 6 provides a summary of results and discusses the methodological and policy issues raised in Chapter 2-5. From a methodological point of view, in this thesis, a dynamic programming approach is used which is a suitable approach for invasive plant management. There have been several studies using a dynamic programming method. However, I make a contribution to the literature by performing a dynamic programming analysis in which two different categories of control strategies are considered, each with different dynamics. The first category concerns control strategies that have to be selected on an annual basis. The second category is a once-and-for-all choice, meaning that once applied they will not have to be repeated in the future. Next, I develop a stochastic dynamic optimisation model to analyse whether including stochastic effects of biological control changes the optimal control strategies adopted. This thesis makes new contributions to the methodologies applied in the literature so far, as a stochastic optimisation model is set up with a discrete decision variable consisting of 62 feasible combinations of integrated control strategies. Moreover, I analyse whether the introduction of a biological control agent in a managed compartment can cause a spillover effect that causes extinction of a wild endemic species in a natural compartment. Previous studies showed that introducing a biological agent in a managed compartment can cause spillover effects on a natural compartment. I, however, make a new contribution to the literature by introducing a novel modelling approach to analyse the conditions under which the dispersal of a biological control agent from a managed to a natural system results in a spillover effect, threatening biodiversity. In the model, two compartments are distinguished: a managed compartment where locally a herbivore is introduced to control a weed, and a natural compartment where the same herbivore species can attack a wild plant species, in that way affecting the dynamics between different species. The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment, herbivores attack a non-target host plant species which competes with another plant species or group of species. The main processes in the model are herbivory, competition and dispersal. Finally, cost-effectiveness of controlling herbivores in the natural compartment is analysed. Related studies have focused on similar economic questions. In this thesis, however, a new contribution is made by finding the optimal level of control in a system which takes into account competition, herbivory, dispersal and control, for a two compartment system as described above.

I conclude that bioeconomic modelling is an important tool in analysing optimal management strategies for the control of invasive species and that annual and once and for all

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choices need to be integrated in the analysis. A stochastic approach is appropriate but does not necessarily lead to different results, depending on the parameter values and the setup of the model. Finally, the method illustrates that an integrated analysis of the economic system and the ecological system is required to assess the risk of extinction of natural plant species. This risk depends on species interactions which in this thesis are competition, dispersal and herbivory. I conclude that a control measure can protect the desirable wild plant species and increase benefits obtained from the ecosystem. The optimal level of control depends on the processes such as competition, dispersal and herbivory.

For the policy implications, I conclude that there are several strategies to control invasive species, which can be integrated combinations of control options. The optimal strategy depends on the costs and benefits of the control options. In the case study for the Californian thistle I found that the optimal strategy is a combination of methods and that chemicals can be replaced by more environmental friendly methods at a cost of less than 2% of net present value. For the interaction between agricultural and natural system I conclude that introducing a biological agent to the agricultural system can cause extinction of a desirable plant in the natural system. The main processes are competition, herbivory and dispersal. These processes are important and need to be analysed in detail before introducing the biological agent. I conclude that the optimal strategy to control the introduced biological agent also depends on interaction of species through competition, dispersal and herbivory.





Invasieve soorten zijn één van de meest significante bedreigingen voor biodiversiteit en landbouwproductiesystemen. De meerderheid van onze natuurlijke ecosystemen ondervinden schade door invasieve soorten. Uitheems onkruid is de schadelijkste vorm van invasieve soorten en leidt wereldwijd tot hoge economische schade door productieverliezen en de kosten om invasies te beheersen.

Dit proefschrift heeft twee belangrijke doelstellingen. Het eerste doel is om het beheer van een invasieve plant in een landbouwsysteem te analyseren. Ik gebruik de Californische distel in Nieuw Zeeland als case study, om landbouwers in Nieuw Zeeland te assisteren bij het bepalen van de meest rendabele strategieën voor het beheer van de Californische distel in hun weilanden. Door een systematische analyse met vernieuwende modelleringstechnieken toe te passen draag ik bij aan de literatuur over invasieve soorten. Het tweede doel van dit proefschrift is om de negatieve externaliteiten voor ecosystemen, die veroorzaakt worden door het beheer van invasieve soorten, te bestuderen. Om het eerste doel te bereiken, heb ik zowel deterministische als stochastische dynamische programmeringsmodellen gebruikt, om de meest rendabele methodes te vinden om het probleem van de Californische distel aan te pakken. Voor het tweede doel, heb ik een ecologisch en bioeconomisch model voor het landbouwsysteem en het gerelateerde natuurlijke systeem ontwikkeld.

De case study concentreert zich op Nieuw Zeeland, een land met zeer diverse en waardevolle natuurlijke rijkdommen. Nieuw Zeeland wordt beschouwd als een van de gebieden met de hoogste graad van invasies ter wereld. Veel uitheems onkruid belemmert de landbouw in weidegebieden in Nieuw Zeeland en één van de belangrijkste hiervan is de Californische distel (*Cirsium arvense*). De Californische distel is een zeer lastig onkruid omdat het moeilijker is te controleren dan andere invasieve planten en het wordt als één van de meest schadevolle ter wereld beschouwd.

Om de doelstellingen van dit onderzoek te bereiken, beantwoorden Hoofdstukken 2-5 van dit proefschrift verscheidene onderzoeksvragen.

Hoofdstuk 2 onderzoekt de beste modelleringsbenadering om het probleem van Californische distel aan te pakken en bestudeert de meest rendabele strategieën. Om het probleem van Californische distel in Nieuw Zeeland aan te pakken zijn verscheidene beheersopties beschikbaar. Ik bekijk geïntegreerde strategieën van onkruidbeheer (IWM) die 4-chloor-2-methylphenoxy (MCPA), 4-(4-chloor-2-methylphenoxy) (MCPB), intensief weiden, mycoherbicides, het maaien in Januari en het maaien in Maart en het introduceren van insectherbivoren (*Apion Onopordi*) met elkaar combineren. Combinaties van deze zeven beheersopties geven 62 uitvoerbare IWM strategieën. Een deterministisch dynamisch programmeringsmodel is ontwikkeld om de meest rendabele IWM strategieën te bestuderen. Ik gebruik een deterministisch dynamisch programmeringsmodel dat een groot aantal besluitvariabelen behandelt die verdeeld zijn in twee categorieën: omkeerbaar en onomkeerbaar. Mijn onderzoek toont aan dat de optimale geïntegreerde strategie van

onkruidbeheer (IWM) het toepassen van een combinatie van beheersopties is, zelfs bij lage dichtheden van de Californische distel. De analyse toont aan dat de introductie van insectherbivoren (onopordi Apion) als biologisch bestrijdingsmiddel leidt tot een verhoging van de netto contante waarde (NPV) van maximaal 2 procent. Dit impliceert dat insectherbivoren kunnen worden uitgesloten als beheersoptie als de kosten lager dan 2 procent van de NPV zijn; dit staat gelijk aan de alternatieve kosten van het vermijden van ecologische risico's met betrekking tot toepassen van biologische bestrijdingsmiddelen. De analyse toont aan dat een combinatie van inzetten van insectherbivoren, het geïntensifieerd weiden en MCPA optimaal is bij lage niveaus van disteldichtheid. Voor hoge disteldichtheid is het optimaal om ook het maaien in Januari en mycoherbicides toe te passen. Daarnaast toon ik ook aan dat het uitsluiten van herbiciden als beheersoptie de NPV met maximaal 2 procent verlaagt. Daarom kunnen de herbiciden door meer milieuvriendelijke opties worden vervangen bij een kostenniveau van minder dan 2 procent van de NPV.

Hoofdstuk 3 modelleert het probleem van de Californische distel wanneer de biologische bestrijdingsmiddelen stochastische gevolgen voor de distel hebben en analyseert de beste beheersopties bij deze stochastische opzet. Om die reden ontwikkel ik een stochastisch dynamisch programmeringsmodel, waarin de effecten van twee biologische bestrijdingsmiddelen (d.w.z. insectherbivoren en mycoherbicides) voor de invasieve species stochastisch zijn. Voor de structuur van het model en de aangenomen parameter-waardes, laten de resultaten zien dat ondanks de stochastische effecten van de twee biologische bestrijdingsmiddelen, het nog steeds optimaal is om hen te introduceren in de weilanden in Nieuw Zeeland, aannemend dat zij geen ongunstig effect op andere soorten hebben. Het introduceren van een stochastisch effect van de insectherbivoren beïnvloedt de optimale strategie niet. Nochtans toont de analyse aan dat in het geval van stochasticiteit, mycoherbicides slechts bij hoge disteldichtheid worden geïntroduceerd. Dit betekent dat als stochasticiteit niet zou zijn overwogen, mycoherbicides reeds bij lagere disteldichtheid geïntroduceerd zouden zijn. De analyse laat zien dat voor de meeste disteldichtheden (dichtheid tussen 17 en 61 shoot/m<sup>2</sup>), wanneer de chemische producten (d.w.z. MCPA en MCPB) in de combinatie van beheersopties worden opgenomen, de beste IWM strategieën MCPA, intensief weiden en toepassen van insectherbivoren zijn. Wanneer de chemische producten worden uitgesloten, zijn, voor de meeste dichtheden, mycoherbicide en het maaien in Januari en Maart de beste IWM strategieën. Het uitsluiten van chemische producten en het toepassen van meer milieuvriendelijke opties kost maximaal 1,3 procent van de NPV.

Hoofdstuk 4 bestudeert het effect van het toepassen van een biologisch bestrijdingsmiddel, om invasieve soorten in een landbouwsysteem te verminderen, met het risico op uitsterven van wilde plantensoorten. Biologische bestrijdingsmiddelen, zoals insectherbivoren (bv. snuitkevers), die gebruikt worden bij het bestrijden van invasieve soorten in landbouwsystemen kunnen zich verspreiden naar andere delen van het ecosysteem en daar schade toebrengen aan wenselijke soorten. Ik stel een ecologisch model op met twee

afzonderlijke compartimenten: 1) een beheerd compartiment (d.w.z. landbouwgrond) waar herbivoren (d.w.z. een biologisch bestrijdingsmiddel) wordt geïntroduceerd om een invasieve plant (d.w.z. onkruid) te beheren, en 2) een natuurlijk compartiment (bv. een onbeheerd systeem) waar dezelfde herbivoor schade kan aanrichten aan wilde, wenselijke, plantensoorten. De twee herbivoor bevolkingen zijn verbonden, waardoor de herbivoor zich kan verspreiden van het ene compartiment naar het andere. In het natuurlijke compartiment vallen de herbivoren andere plantensoorten aan die niet het doelwit zijn en concurreren met een andere soort of soorten.

De belangrijkste processen in het model zijn herbivorie, concurrentie en verspreiding. De resultaten tonen aan dat het mogelijk is dat de herbivoor zich vestigt en zelfs wilde soorten in het natuurlijke compartiment bedreigt met uitsterven. Het risico op biodiversiteitsverlies is het hoogst als de verspreidingsgraad van herbivoren tussen het natuurlijke en beheerd compartiment hoog is, en als de inheemse plant in het natuurlijke compartiment sterk concurreert met andere plantensoorten. Daarom kan, wanneer de verspreidingsgraad hoog is, de introductie van herbivoren tot biodiversiteitsverlies leiden in het natuurlijke compartiment. Een interessant fenomeen is het bestaan van een niet-lineair verband tussen het aantal herbivoren en onkruidichtheid. Als de aanvalscoefficiënt van de herbivoren in het beheerde compartiment stijgt, stijgt de dichtheid van herbivoren tot het punt waar de onkruidichtheid erg laag wordt door herbivorie, met als resultaat dat de dichtheid van herbivoren weer omlaag gaat. Dit betekent dat een gematigde aanvalscoefficiënt in het beheerde compartiment hoge herbivoor dichtheden kan veroorzaken en hoge externaliteiten kan produceren. Ik concludeer ook dat de overloop van herbivoren van het beheerde naar het natuurlijke compartiment het uitsterven van een wilde plantensoort kan veroorzaken, zelfs als sommige parameterwaarden, zoals de aanvalscoefficiënt op onkruid, lage risico's suggereren.

Hoofdstuk 5 analyseert, van een economisch standpunt, de beste optie om een wilde plantensoort te beschermen wanneer het aangevallen wordt door herbivoren die zich verspreiden van en naar het landbouwgebied. Ik ontwikkel een bioeconomisch model waarin, zoals hierboven besproken, twee compartimenten worden onderscheiden. De compartimenten, de interactie tussen de soorten en de verspreiding zijn gelijk aan het ecologische model dat in Hoofdstuk 4 wordt gebruikt. In dit hoofdstuk echter, introduceer ik een beheersmaatregel die de herbivoordichtheid in het natuurlijke compartiment vermindert, waardoor de wilde plantensoort tegen herbivorie beschermd is. Dit maakt het mogelijk om het verband tussen de meest rendabele beheersniveaus en de belangrijkste ecologische en economische parameterwaarden te begrijpen. Hier zijn bij het meten van kosteneffectiviteit niet alleen economische voordelen van landbouw inbegrepen, maar ook de voordelen van het behoud van biodiversiteit. Ik toon aan dat als de wilde inheemse plant in het natuurlijke compartiment een hogere concurrentiedruk heeft, de marginale opbrengsten van beheerverhoging stijgen, en daarmee het optimale beheersniveau ook. Als de aanvalscoefficiënt van herbivoren op de wilde inheemse plant stijgt, stijgt ook het

geboortecijfer van de herbivoren. Daarom verwacht men dat zonder beheer de herbivoordichtheid zal stijgen. Dit zou resulteren in een lagere dichtheid van wilde inheemse planten en daardoor leiden tot lagere baten. In dit geval kan het beheer van herbivoren de baten verhogen. Het beheer verhoogt de dichtheid van de wilde inheemse planten door de dichtheid van herbivoren te verminderen tot het optimale niveau waar de marginale kosten en baten van beheer gelijk zijn. Als de aanvalscoefficiënt op de wilde inheemse planten stijgt, daalt de dichtheid van wilde inheemse planten, en daardoor stijgen de marginale baten van beheer. Om het evenwicht, in het geval van stijgende aanvalscoefficiënten te bereiken, zal het beheersniveau van herbivoren moeten stijgen. Het optimale beheer, echter, reageert anders op veranderingen in de aanvalscoefficiënt op de invasieve plant. Als deze aanvalscoefficiënt stijgt, daalt de onkruidichtheid. Als de voedselbron van de herbivoren (d.w.z. onkruid) vermindert, vermindert ook de dichtheid van de herbivoren in het beheerde compartiment. Een lagere dichtheid van herbivoren in het beheerde compartiment resulteert in een lagere overloop van herbivoren naar het natuurlijke compartiment. Daardoor vermindert de aanval op de wilde inheemse plant. Dit verlaagt de marginale baten van het verhogen van het aantal wilde inheemse planten door beheer. Daarom daalt ook het optimale niveau van beheer. Verder is ook aangetoond dat de optimale beheersniveaus grotendeels van de waarden van de economische parameters afhangen. Bijvoorbeeld, er is een veel hoger beheersniveau nodig wanneer de economische waarde van de wilde soorten die door herbivoren wordt aangevallen hoog is. In dat geval, worden namelijk de marginale voordelen van het verhogen van het aantal wilde inheemse planten groter.

Hoofdstuk 6 geeft een samenvatting van resultaten en bespreekt de methodologische en beleidskwesties die in hoofdstukken 2 tot en met 5 worden geïntroduceerd. Methodologisch gezien, wordt in dit proefschrift een dynamische programmeringsbenadering gebruikt die een geschikte benadering is voor de analyse van invasieve soortenbeheer. Er zijn verscheidene studies geweest die een dynamische programmeringmethode hebben gebruikt. Nochtans lever ik een bijdrage aan de literatuur door een dynamische programmeringsanalyse uit te voeren waarin twee verschillende categorieën van beheerstrategieën, elk met een verschillende dynamiek, worden overwogen. De eerste categorie betreft beheerstrategieën die op een jaarlijkse basis moeten worden geselecteerd. De tweede categorie is een voor-eens-en-altijd keuze, wat betekent dat zodra deze beheersstrategie is toegepast, dit in de toekomst niet herhaald hoeft te worden. Daarna ontwikkel ik een stochastisch dynamisch optimaliseringmodel om te analyseren of het meerekenen van stochastische gevolgen van biologisch beheer de optimale beheerstrategieën verandert. Dit proefschrift levert nieuwe bijdragen aan de methodologie die in de literatuur tot dusver wordt toegepast, aangezien een stochastisch optimaliseringmodel wordt opgesteld met een discrete besluitvariabele, bestaand uit 62 uitvoerbare combinaties van geïntegreerde beheerstrategieën. Verder analyseer ik of het toepassen van een biologisch bestrijdingsmiddel in een beheerd compartiment een overloopeffect kan veroorzaken dat het uitsterven van wilde inheemse soorten in een

natuurlijk compartiment als gevolg heeft. Vorige studies toonden aan dat het introduceren van een biologisch bestrijdingsmiddel in een beheerd compartiment overloopgevolgen voor een natuurlijk compartiment kan veroorzaken. In dit proefschrift lever ik echter een nieuwe bijdrage aan de literatuur door een nieuwe modelleringbenadering te introduceren om de voorwaarden te analyseren waaronder de verspreiding van een biologisch bestrijdingsmiddel in een overloopeffect van een beheerd naar een natuurlijk systeem resulteert, dat vervolgens biodiversiteit bedreigt. In het model worden twee compartimenten onderscheiden: een beheerd compartiment waar plaatselijk herbivoren worden geïntroduceerd om een onkruid te beheren, en een natuurlijk compartiment waar dezelfde herbivoren een wilde plantensoort kan aanvallen; dit beïnvloedt de dynamiek tussen de verschillende soorten. De twee herbivorenpopulaties zijn verbonden door verspreiding, waardoor de natuurlijke vijand van één compartiment naar het andere kan overlopen. In het natuurlijke compartiment vallen de herbivoren een inheemse plantensoort aan die met een andere plantensoort of groep plantensoorten concurreert. De belangrijkste processen in het model zijn herbivorie, concurrentie en verspreiding. Tot slot wordt de kosteneffectiviteit van het beheren van herbivoren in het natuurlijke compartiment geanalyseerd. Verwante studies hebben zich op gelijke economische vragen geconcentreerd. In deze thesis, echter, wordt een nieuwe bijdrage geleverd door het optimale niveau van beheer in een systeem te vinden dat rekening houdt met concurrentie, herbivorie, verspreiding en beheer, voor een twee-compartimentensysteem zoals hierboven beschreven.

Ik concludeer dat bioeconomische modellering een belangrijk hulpmiddel is in het analyseren van optimale beheersstrategieën van invasieve soorten en dat jaarlijkse en voor-eens-en-altijd keuzes beide in de analyse moeten worden geïntegreerd. Een stochastische benadering is correct maar leidt niet noodzakelijk tot andere resultaten, afhankelijk van de parameterwaarden en de constructie van het model. Tot slot illustreert de methode dat een geïntegreerde analyse van het economische systeem en het ecologische systeem vereist is om het risico van uitsterven van natuurlijke plantensoorten te analyseren. Dit risico hangt af van de interactie tussen soorten die in dit proefschrift gevormd worden door concurrentie, verspreiding en herbivorie. Ik kom tot de conclusie dat een beheersmaatregel de wenselijke wilde plantensoorten kan beschermen en de voordelen behaald uit het ecosysteem kan verhogen. Het optimale niveau van beheer hangt van de processen zoals de concurrentie, verspreiding en herbivorie af.

Wat betreft de beleidsimplicaties van mijn onderzoek, kom ik tot de conclusie dat er verscheidene strategieën zijn om invasieve soorten te beheren, die geïntegreerde combinaties kunnen zijn. De optimale strategie hangt van de kosten en baten van de beheersopties af. In de case study van de Californische distel vond ik dat de optimale strategie een combinatie van methodes is en dat de chemische producten door meer milieuvriendelijke methodes kunnen worden vervangen ten koste van minder dan 2% van de netto contante waarde. Wat betreft de interactie tussen landbouw en het natuurlijk systeem concludeer ik dat het

toepassen van een biologisch bestrijdingsmiddel bij een landbouwsysteem kan leiden tot het uitsterven van een wenselijke plant in het natuurlijke systeem. De belangrijkste processen zijn concurrentie, herbivorie en verspreiding. Deze processen zijn belangrijk en moeten in detail worden geanalyseerd alvorens een biologisch bestrijdingsmiddel wordt toegepast. Ik kom tot de conclusie dat de optimale strategie om het toegepaste biologische bestrijdingsmiddel te beheren ook van de interactie tussen de soorten door concurrentie, verspreiding, en herbivorie afhangt.

Morteza Chalak Haghighi was born on 19th September 1974 in Shiraz, Fars Province, Iran. In 1993 he entered Gorgan University to study Rangeland and Watershed Management Engineering, and graduated as top student in the Bachelor of Science (BSc) in 1997. He entered Tehran University to obtain his Master of Science (MSc) in Range Management in 1998. He graduated with honours in 2000 as the top student in the MSc.

In October 2002 he entered Wageningen University and enrolled in a PhD program at the Economics of Consumer and Households group. For his thesis, *Economics of controlling invasive species*, he chose New Zealand as a case study. In 2005 he visited New Zealand to complete the data collection and field research for his PhD. There, he collaborated with staff at Massey University, Graeme Bourdôt at Lincoln Research Centre and Dave Leathwick at Agresearch Centre. On his return to Wageningen University he changed his research group and started to work with the Environmental Economics and Natural Recourses group. During this research he followed his PhD education program at the Mansholt Graduate School (MG3S) and completed the course work. He has been a member of the Education Committee of Mansholt Graduate School (2003-2006) and PhD Council (2004-2006).

**Publications:**

- Chalak-Haghighi, M., Ruijs, A., Ierland, E.C. van, 2008. Management strategies for an invasive weed: a dynamic programming approach for Californian thistle in New Zealand. *New Zealand Journal of Agricultural Research* 51, 409-424.
- Chalak-Haghighi, M., Ruijs, A., Ierland, E.C. van, Forthcoming. On the economics of controlling an invasive plant by a stochastic biological control agent. *International Journal of Environmental Technology and Management*.
- Jafari, M., Chalak-Haghighi, M., Habibian, S.M., Azarnivand, H., 2003. Assessing some *Atriplex Lentiformis* effects on vegetation characteristics in planted land. *Iranian Journal of Natural Resources* 56(3), 301-307.

## Completed Training and Supervision Plan



Description	Institute / Department	Year	ECTS*
<b>Courses:</b>			
Microeconomics	Wageningen University, the Netherlands	2002	6
Econometrics I	Wageningen University, the Netherlands	2003	6
Research Methodology: Designing and conducting a PhD research project	Mansholt Graduate School of Social Sciences (MG3S)	2003	3
Mansholt Introduction Course	MG3S	2003	1.5
Quantitative Research Methodology and Statistics	Wageningen University, the Netherlands	2003	6
Macroeconomics and International Trade	Wageningen University, the Netherlands	2003	6
Advanced Econometrics	Wageningen University, the Netherlands	2003	6
Techniques for Writing and Presenting a Scientific Paper	Wageningen University, the Netherlands	2004	1.1
Bio-economic Modelling	MG3S	2004	3
Uncertainly Modelling and Analysis	Research School for Socio-Economic and Natural Sciences of the Environment, the Netherlands	2006	2
<b>Presentations at Conferences and Workshops:</b>			3
Mansholt PhD day and Chain and Networks Conference Doctoral Symposium, Wageningen, the Netherlands		2006	
World Congress of Environmental Resource Economists , Kyoto, Japan		2006	
Mansholt PhD day, Wageningen, the Netherlands.		2007	
European Association of Environmental and Recourse Economists Conference, Thessaloniki, Greece		2007	
<b>Teaching and Supervision Activities</b>			1
Supervision of "Environmental Economics for Environmental Sciences" Course	Wageningen University, the Netherlands	2006	
<b>Total (minimum 30 ECTS)</b>			<b>44.6</b>

\*One ECTS on average is equivalent to 28 hours of course work