Social-ecological modelling of potato late blight

Managing crop resistance in disease control

Francine Pacilly

Propositions

1. Sustainable management strategies of potato late blight can only be identified by using a social-ecological systems approach.
   (this thesis)

2. The use of crop resistance in late blight control is only sustainable when combined with resistance management.
   (this thesis)

3. Research results by themselves cannot be used as policy instrument.

4. As long as education is split into disciplines, social-ecological research will only slowly advance.

5. All PhD students should take a pet to release stress.

6. Taxes on air transport should be implemented worldwide.

Propositions belonging to the thesis, entitled

'Social-ecological modelling of potato late blight – Managing crop resistance in disease control'

Francine Pacilly

Wageningen, 4 September 2018

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Abstract

Social-ecological systems are a case of complex adaptive systems. They consist of many components that interact across temporal and spatial scales. The system's overall behaviour emerges from the interactions between the different components, while these components adapt to each other and to the environment. In this thesis, potato late blight control is used as a model system. Systems methods are used to analyse its behaviour and contribute to the development of sustainable disease management strategies.

Late blight, caused by *Phytophthora infestans*, is one of the main threats in potato production worldwide; in the Netherlands, high potato density and favourable weather conditions result in frequent outbreaks of the disease. Crop resistance could play an important role in sustainable disease control by reducing chemical fungicide inputs. However, due to the rapid adaptation of *P. infestans*, there is a risk that the resistance is overcome by the pathogen. The overall disease incidence in the landscape is influenced by spatial biophysical processes as well as crop management strategies of farmers who are influenced by their socio-institutional environment. To analyse the social-ecological interactions a collection of complementary methods was used.

In-depth interviews with farmers, breeders and other experts increased understanding of the Dutch potato sector and of factors involved in decision making on late blight control. Fuzzy cognitive mapping showed that social and ecological processes are tightly linked by various feedback loops. Both an increase in stakeholder cooperation and a change in market demands towards resistant cultivars could improve sustainability of late blight management. In contrast, policies restricting the use of fungicides would result in increased disease severity if no alternative strategies were implemented, which would require social-institutional support and facilitation.

Agent-based modelling (ABM) was used to (i) analyse crop-disease interactions affected by management strategies at the landscape level, (ii) analyse social-ecological interactions between farmer behaviour and disease dynamics and (iii) communicate the dynamics in the complex system to stakeholders. Results showed that increasing the fraction of resistant potato fields strongly reduced late blight incidence in a landscape. However, resistance breakdown could occur by emergence and spread of a new virulent strain. It was found that low as well as high proportions of fields with the resistant variety could increase durability of resistance. The ABM showed that resistance breakdown is the result of interactions between management strategies of farmers, the weather conditions and the allocation of potato varieties in the landscape. Several resistance management strategies were identified that could potentially be effective to increase resistance durability, including (reduced) use of fungicides on all resistant or all susceptible fields, growing a resistant variety with multiple resistance genes (instead of single-gene resistant varieties) and immediate haulm destruction of resistant fields after infection with the virulent strain.

ABM-based scenarios were used as learning tool in workshops with farmers. Scenarios of disease dynamics at the landscape level increased awareness that collective action is needed to prevent emergence and spread of virulent strains. Significant differences in perceptions on disease control were found before and after the workshop as well as between organic and conventional farmers. It was concluded that the workshop increased farmers' knowledge of the system and served as a good starting point for discussions among actors.

Keywords: *Phytophthora infestans,* social-ecological systems, agent-based modelling, resistance management, participatory modelling, cropping patterns, host-pathogen interaction, complex adaptive systems

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Chapter 1

General introduction

1.1 Complex adaptive systems

Avoiding yield losses of food crops has been identified as one of the priorities in securing food availability for the increasing global human population. These losses are caused by insufficient or unbalanced supply of water and nutrients, damage due to weeds, pests and diseases, or by weather-related events (Lobell et al., 2009). Emerging pests and diseases are one of the main threats in agriculture (Anderson et al., 2004). Spread of these diseases is affected by biophysical processes related to crops and pathogens as well as decision-making processes on crop management.

Managed ecosystems can be described as complex since they are characterised by dynamics at multiple spatial and temporal scales and a multitude of interactions (Matthews, 2006). These dynamics concern social as well as biophysical elements. The systems can therefore be described as social-ecological systems which are characterised by interactions and feedback mechanisms between humans and their environment (Schlüter et al., 2012). Social-ecological systems are a case of complex adaptive systems (CAS). The key element of CAS is that patterns at system level emerge from interactions between individual components (Holland, 2006). Analysing coupled human and environmental systems showed that these exhibit nonlinear dynamics with thresholds, reciprocal feedback loops, time lags, resilience, heterogeneity, and surprises (Liu et al., 2007). Besides complex, these systems are also adaptive. For example humans can observe the state of the world and change their behaviour in new ways, and biophysical systems can cross tipping points in their behaviour. A CAS-approach (considering the system under study as a CAS) can increase understanding of the system behaviour by analysing the interactions between system components. Understanding of the mechanisms underlying system behaviour can contribute to the design of effective management strategies. The CAS-approach has been applied to many systems such as ecosystems (Levin, 1998), land-use systems (Parker et al., 2003) and supply networks (Choi et al., 2001). A central idea about CAS is that although systems can strongly differ, the mechanisms and interaction patterns that lead to emergent behaviour can be similar and therefore the findings from one study may be relevant in other systems. A number of methods are available that analyse the system dynamics from different perspectives and these can be generally applied dependent on the context and purpose of the study.

This thesis project is part of a larger program where the CAS-approach was applied to a number of case studies. In this thesis the CAS-approach was used for analysing the social-ecological system of potato late blight. Control of late blight is the result of interactions between involved actors (e.g. breeders, farmers and consumers) through social networks, as well as between plants and pathogens through disease epidemiology (Figure 1.1). Farmers play a key role in this system since they make decisions on crop management but also respond to changes in the social and biophysical environment (Edwards-Jones, 2006; Feola and Binder, 2010). Potato late blight is analysed as a model system for studying multi-level social-ecological processes and for finding options for improved management and governance of crop-disease interactions in landscapes. For the development of sustainable management strategies it is important that actors involved in decision making understand the complex dynamics in the system. Managing complex adaptive systems requires adaptive governance that focuses on experimentation and learning, and on bringing stakeholders together for collaboration and collective action (Folke et al., 2005).

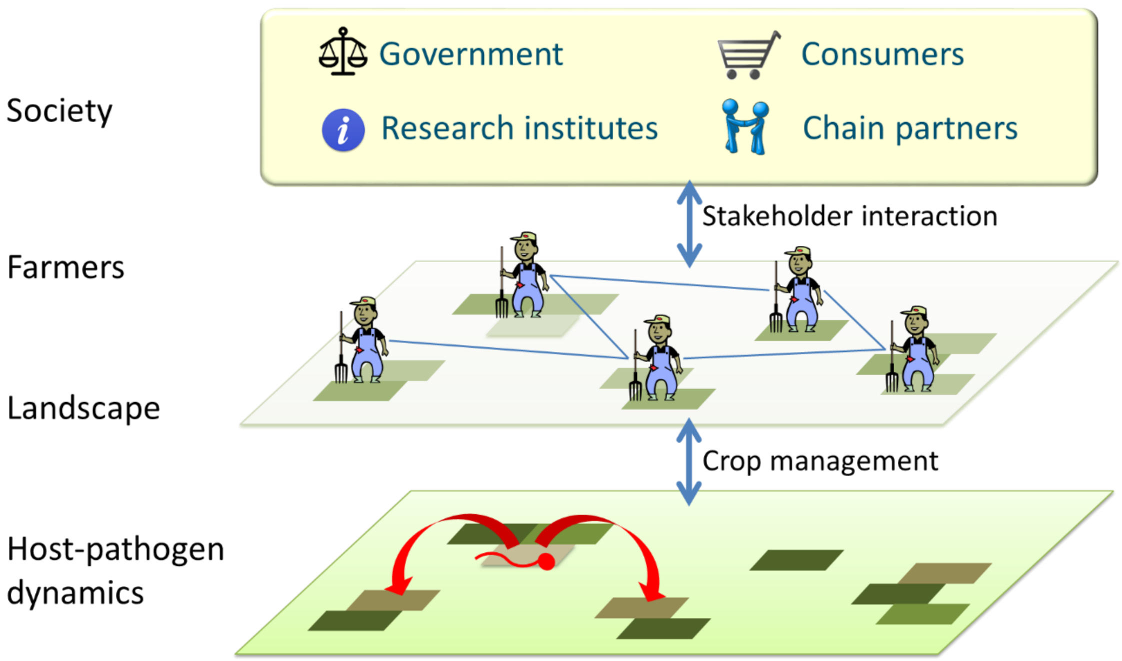

Figure 1.1. Conceptual overview of the social-ecological system of potato late blight.

1.2 Potato late blight

Potato late blight, caused by the oomycete *Phytophthora infestans*, is one of the main diseases in potato (*Solanum tuberosum*) production. *Phytophthora* in Greek means 'plant destroyer' which is an apt name for this aggressive pathogen. A historical catastrophe that shows the devastating effects of this disease occurred in Europe in the mid-nineteenth century. Potatoes originated in South-America and were introduced to Europe in the 16th century, without late blight. Since then potato had become the most important crop in Europe, still free of late blight (Zadoks, 2008). Unfortunately, around 1845 a strain of *P. infestans* arrived in Europe, which immediately resulted in severe late blight outbreaks. Especially in Ireland, where about one third of the population relied on this cheap crop for food, the impact was enormous. The late blight epidemic led to the 'Irish potato famine' (O'Neill, 2009). During the Irish potato famine one million people died as a result of starvation and another million emigrated to Britain, the U.S. and Canada. The Irish potato famine remains one of the most striking examples of how a pathogen can have huge impacts on the environment and society. Today late blight is still one of the main threats in potato production worldwide and the global costs (related to control and losses) have been estimated at €9 billion per year (Haverkort et al., 2016). The current issues related to late blight control are described in more detail for the Netherlands in Section 1.4.

The pathogen has a number of characteristics that makes it so aggressive. During the growing season *P. infestans* can reproduce rapidly because of its short life cycle and high spore production. The spores are dispersed by wind, so in case of favourable weather a late blight epidemic can spread over large areas in a short time (Zwankhuizen and Zadoks, 2002). Infection with late blight results in foliage death and potato tuber rot in the field and in storage. Besides an asexual life cycle the pathogen is also able to reproduce sexually, resulting in the formation of oospores which can survive in the soil for a number of years (Drenth et al., 1995). Sexual reproduction can only occur when both mating types (called A1 and A2) of *P. infestans* are present. Before 1980 the worldwide population of *P. infestans* (except for Mexico) consisted of only one mating type (Cooke et al., 2011). After the introduction of the second mating type *P. infestans* was also able to reproduce sexually which led to a diverse pathogen population and increased adaptability to its host and the environment. Due to the high plasticity of pathogenicity in the genome of *P. infestans* new strains can also emerge as a result of mutations in the asexual life cycle during the growing season (Goodwin et al., 1995). In cold temperature zones, *P. infestans* survives between seasons by the formation of oospores or in infected potato tubers (Zwankhuizen et al., 1998). In potato tubers, initial infection sources can be the result of infected seed potatoes, discarded potatoes on refuge piles or remaining tubers in the soil after harvesting (volunteer plants).

The weather is the most important factor influencing spread of the disease. Favourable weather conditions for the disease include moderate temperatures and high humidity. As a result late blight is mainly a problem in rain-fed production systems with a moderate climate. The effect of weather variables on the developmental stages of *P. infestans* has been well studied and more information can be found in the following references (Andrade-Piedra et al., 2005; Crosier, 1934; Mizubuti et al., 2000; Mizubuti and Fry, 1998).

1.3 Crop resistance

The large-scale use of susceptible varieties makes the system vulnerable for spread of the disease and control of the disease control largely depends on the heavy use of fungicides. Crop resistance could play an important role in the development of sustainable disease management strategies. In the literature several types of resistance are described including quantitative and qualitative resistance (Fry, 2008; Lo Iacono et al., 2013; Plich et al., 2016; Rietman et al., 2012). The first type is also referred to as field or partial resistance. It does not provide complete protection, but can reduce disease severity by slowing down the infection process when the disease pressure is not too large. These varieties can have for example better physical barriers or induced chemical defences to slow down the infection. In qualitative resistance, the resistance is the result of major resistance genes (gene for gene interaction) and non-compatible pathogens are unable to infect the host (Flor, 1971). In this type of resistance, proteins released by the pathogen are recognized by the host, resulting in a defence response making the host immune. Pathogen adaptation, for example by mutation, can lead to changes in these proteins resulting in a virulent pathogen that is not detected by the host and can cause an infection. Experimental data showed that virulence could rapidly evolve within clonal lineages of *P. infestans* which suggests a high mutation rate (Goodwin et al., 1995). Resistance breakdown is the result of an increase in the fraction of virulent strains in the pathogen population. This thesis focuses on crop resistance based on major resistance genes.

Breeding for resistant varieties started in the beginning of the twentieth century when resistant genes (R-genes) were discovered in the closely related species *Solanum demissum* (Fry, 2008). Unfortunately, when these resistant varieties came to be more widely used, this increased selection of *P. infestans* strains with compatible virulence genes. As a result, the eleven R-genes from *S. demissum* have been broken by the pathogen around 1950. Introgressing resistance genes from wild relatives by classical breeding is a time-consuming process. The pre-breeding phase can take 15-20 years in which genitors are developed with the resistance genes and with sufficient level of agronomic traits as a base for commercial breeding programs (Hermsen and Ramanna, 1973). It then takes another 10 years of commercial breeding before a variety can be successfully registered and marketed (Tiemens-Hulscher et al., 2013).

Late blight resistance based on single resistance genes is however easily overcome by the pathogen. Breeders can include combined (stacked) resistance genes from different sources, but this is more demanding (costs, time). It is also uncertain how many resistance genes are needed to prevent break-down of resistance (Tan et al., 2010). In addition, resistance management strategies need to be developed and applied to increase resistance durability.

1.4 Case study area: the Netherlands

The Netherlands are a large producer of seed, ware and starch potatoes and the production contributes M€800 to the Dutch economy each year (Haverkort et al., 2008). Because of the high potato density and favourable weather for the disease, late blight is one of the main problems in potato production. The yearly costs of late blight are estimated at M€125. This is due to costs for fungicide application and losses in yield. Conventional agriculture heavily relies on the frequent application of fungicides to control the disease. Fungicides are usually applied on a weekly basis and the number of fungicide applications varies between 10-16 applications during the growing season. Late blight control is responsible for about 50% of the total amount of fungicides used in the Netherlands. The fungicides have a negative effect on the environment due to pollution of groundwater, energy costs for application and negative effects on human health (Haverkort et al., 2008; Haverkort et al., 2016). Since chemicals are not allowed in organic agriculture potato yields can be dramatically low in years with severe outbreaks of the disease (Lammerts van Bueren et al., 2008). The moment and severity of a late blight epidemic is weather dependent and highly variable per year, so organic farmers have to deal with a lot of uncertainty. As a result of late blight outbreaks between 2000 and 2007 the Dutch organic potato production acreage decreased by 20%.

With the aim of reducing the number of initial infection sources and preventing spread of the disease, the Dutch government implemented sanitary regulations (NVWA, 2008). According to these regulations volunteers (self-sown plants) have to be removed and cull piles have to be covered to reduce the number of potential infection sources. Furthermore a policy has been implemented that states that the potato haulm needs to be destroyed at an estimated 5% infection level to prevent spread to neighbouring fields. An inspection has been set up that could fine farmers in case these rules are not followed.

In attempts to improve disease control for organic farmers and to reduce the amount of fungicides in conventional systems, the use of resistant varieties can play a key role (Finckh et al., 2006; Haverkort et al., 2016). Varieties with new late blight resistance genes have been entering the Dutch market since 2007, and have so far mainly been used in organic farming systems. The first generation of new resistant varieties have a moderate yield level and do not meet all the market requirements compared to those of regular (susceptible) varieties (Nuijten et al., 2017). In the project 'Bioimpuls', six commercial breeding companies, Wageningen University & Research, the Louis Bolk-Institute and some 10 farmer breeders joined forces to develop late blight resistant varieties with several new resistance genes through classical breeding (Lammerts van Bueren et al., 2009). The late blight resistant cultivars from this programme aim to serve both organic and conventional markets.

1.5 Problem definition

This thesis focuses on management of potato late blight in the Netherlands. In this system we are dealing with a very aggressive pathogen and an environment that is conducive for disease spread. As a result of the short life cycle, the high rate of spore production and of spore dispersal by wind the disease can spread fast in case of favourable weather conditions. The pathogen can adapt rapidly to changes in its host and the environment. The plasticity of pathogenicity in the genome *P. infestans* suggests a high mutation rate which leads to the ability to overcome both the sensitivity to fungicides and the resistance of potato plants to the disease. Since 1980 both mating types of *P. infestans* are present in the Netherlands. The pathogen is now also able to reproduce sexually and as a result the pathogen has become more aggressive over the last decades (Cooke et al., 2011). Because the potato density in the Netherlands is high and weather conditions are favourable for spread of the disease, late blight is one of the main problems in potato production. In conventional agriculture fungicides are used to control the disease but these are harmful for the environment. In organic agriculture the use of chemicals is not allowed, therefore yields can be dramatically low in years with early outbreaks of the disease. Since no other effective methods are available in disease control the development of resistant varieties is a top priority. However, due to the rapid adaptation of *P. infestans* there is a high risk that the resistance of single-gene varieties is overcome by the pathogen. Breeding for resistance is a time-consuming process and also the number of available resistance genes is limited. Resistance management is therefore required to increase resistance durability and protect these varieties, which have been produced with great cost, from the risk of rapid pathogen evolution.

Furthermore potato late blight control also includes a complex social system. Management of potato late blight involves many different stakeholders such as farmers, breeding companies, traders and the government. For the development and implementation of sustainable management strategies it is therefore important to consider the processes and factors involved in decision making. Since the disease is dispersed by wind the overall disease incidence is affected by all farmers in the landscape. Furthermore the development of resistant varieties is dependent on breeding companies, but the selection and use of potato varieties is mainly determined by the market demands. Sustainable management of the disease therefore requires cooperation between stakeholders in the whole value chain.

1.6 Methodology

A number of methods can be used for increasing understanding of the components and interactions within a social-ecological system. Available methods include in-depth interviews, fuzzy cognitive mapping, agent-based modelling, scenario analysis, participatory modelling, workshops and surveys. These methods focus on different aspects of the complex system. In this thesis they were used to analyse and inform the social-ecological system of potato late blight, to analyse the complex, multi-scale dynamics, and to show these from different perspectives (Figure 1.2).

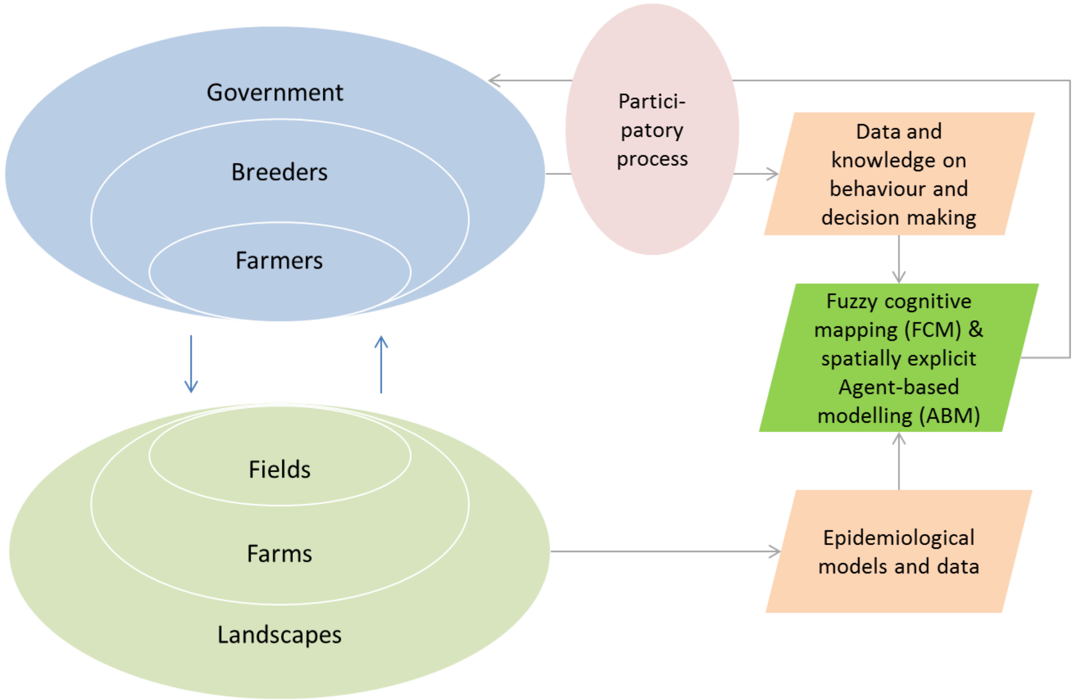

Figure 1.2. Schematic overview of the interacting nested ecological and socio-institutional systems, and the methodology to analyse the social-ecological dynamics in the case of potato-late blight in this thesis.

Modelling is a useful tool for analysing social-ecological systems. Models can increase understanding of the way in which characteristics of the ecological and social system and their interactions determine overall system behaviour. They can provide management advice that takes the coevolving nature of the complex system into account (Schlüter et al., 2012). The modelling tools used in this study were fuzzy cognitive mapping and agent-based modelling. Fuzzy cognitive mapping is a semi-qualitative method that was used to summarise the most important concepts and relationships in the system (Kok, 2009). Fuzzy cognitive mapping is a scenario development methodology, where scenario development is defined as a story about the future that could be told in words or numbers. Fuzzy cognitive mapping makes a link between qualitative (storylines) and quantitative (mathematical models) scenarios.

Agent-based modelling (ABM) has been recognised as highly suitable for representing heterogeneous collections of interacting social and ecological entities in a spatial environment in which biophysical and socio-institutional dynamic processes occur (An, 2012; Gilbert, 2008; Matthews et al., 2007; Schlüter et al., 2012). Agents are autonomous entities that interact with each other and with the environment. Agent-based modelling has the ability to simulate human behaviour by focussing on factors such as heterogeneity, interactions, adaption and learning (Filatova et al., 2013). Applications of agent-based models for simulation of decision-making concerning land-use and land-cover change have a long history and are widely applied (Matthews et al., 2007; Parker et al., 2002). Other agent-based models focus more on the ecological part of land-use systems by simulating the interactions between spatially allocated objects and their management by human agents (Matthews, 2006). Models of coupled social-ecological systems that analyses the interactions and feedback mechanisms between humans and their environment are still scarce (Parker et al., 2008). By developing an agent-based model on the social-ecological interactions on late blight control we aim to contribute to this field of research.

In this thesis agent-based modelling was used for simulating the social-ecological interactions and for increasing understanding of the factors that affect late blight control at the landscape level. As input for model development data was collected on both biophysical and social aspects of late blight control. Management and epidemiology of *P. infestans* have been widely investigated (Fry, 2008) and the existing models and data were used in this study to derive model variables and parameter values. For detailed understanding of the Dutch potato sector interviews were carried out with stakeholders such as farmers, breeding companies and experts. The interviews were used to analyse perceptions on late blight control and to analyse the factors and processes involved in decision-making. The framework on farmers' decision making was based on social theories on human behaviour (Groeneveld et al., 2017; Schlüter et al., 2017) and supported by data from interviews with farmers.

The agent-based model was used in workshops with stakeholders to show the consequences of individual action on larger scales, to increase their understanding of the system behaviour and to show opportunities for change. Participatory modelling has been recognized as a powerful tool to increase actors knowledge of the system and to facilitate learning on complex system dynamics (Barreteau, 2003; Oteros-Rozas et al., 2015; Voinov and Bousquet, 2010; Voinov et al., 2016). To analyse the effect of the workshop questionnaires and surveys were used (Mayer et al., 2014; Voinov and Bousquet, 2010).

1.7 Objectives/ Research questions

General objective

In this research potato late blight control is analysed as a social-ecological system to increase understanding of the system behaviour and to identify factors and processes that could contribute to the development of sustainable disease management strategies. To explore and influence this complex social-ecological system the evolutionary and population dynamics of the pathogen need to be linked to the spatial pattern of allocation of potato varieties and to the interactions in the social network of stakeholders. A collection of methods is used and by applying them to this specific context their usefulness to analyse such a complex social-ecological system is evaluated.

Specific objectives

The specific objectives are:

- To analyse and describe the components, the interactions and feedback mechanisms in the social-ecological system of potato late blight and to identify important drivers (Chapter 2).
- To explore crop-disease interactions at the landscape level by developing spatially explicit agent-based models that include the evolutionary and population dynamics of *P. infestans* and management strategies of farmers (Chapter 3).
- To explore the interactions between farmer behaviour and late blight control by linking a framework on farmer behaviour to populations dynamics of *P. infestans* in an agent-based model (Chapter 4).
- To evaluate the usefulness of agent-based models as learning tools by applying these in participatory settings and by analysing farmer perception on late blight control (Chapter 5).

Research questions

The research questions are:

- How do the interactions between stakeholders, management strategies and population dynamics of late blight affect disease control at the landscape level (Chapter 2)?
- How does landscape composition with respect to spatial deployment of late blight resistant potato varieties and management strategies of farmers affect potato yield, disease incidence and resistance durability (Chapter 3)?
- How do the interactions between farmers' decision making and late blight dynamics affect the use of resistant varieties and resistance durability in response to several scenarios of socio-institutional and economic change (Chapter 4)?
- Can the agent-based model be used as a learning tool for farmers to increase understanding of the system dynamics and how do conventional and organic farmers perceive various strategies in late blight control (Chapter 5)?

1.8 Thesis outline

The outline of this thesis is shown in Figure 1.3. Chapter 2 describes the social-ecological system of potato late blight. To analyse and describe the components, the interactions and feedback mechanisms related to late blight management, three different methods are used; 1) literature search on late blight management, 2) semi-structured interviews with stakeholders and 3) a modelling exercise called Fuzzy Cognitive Mapping (FCM). The FCM summarises the main factors and relations related to late blight control and is used to analyse several management scenarios.

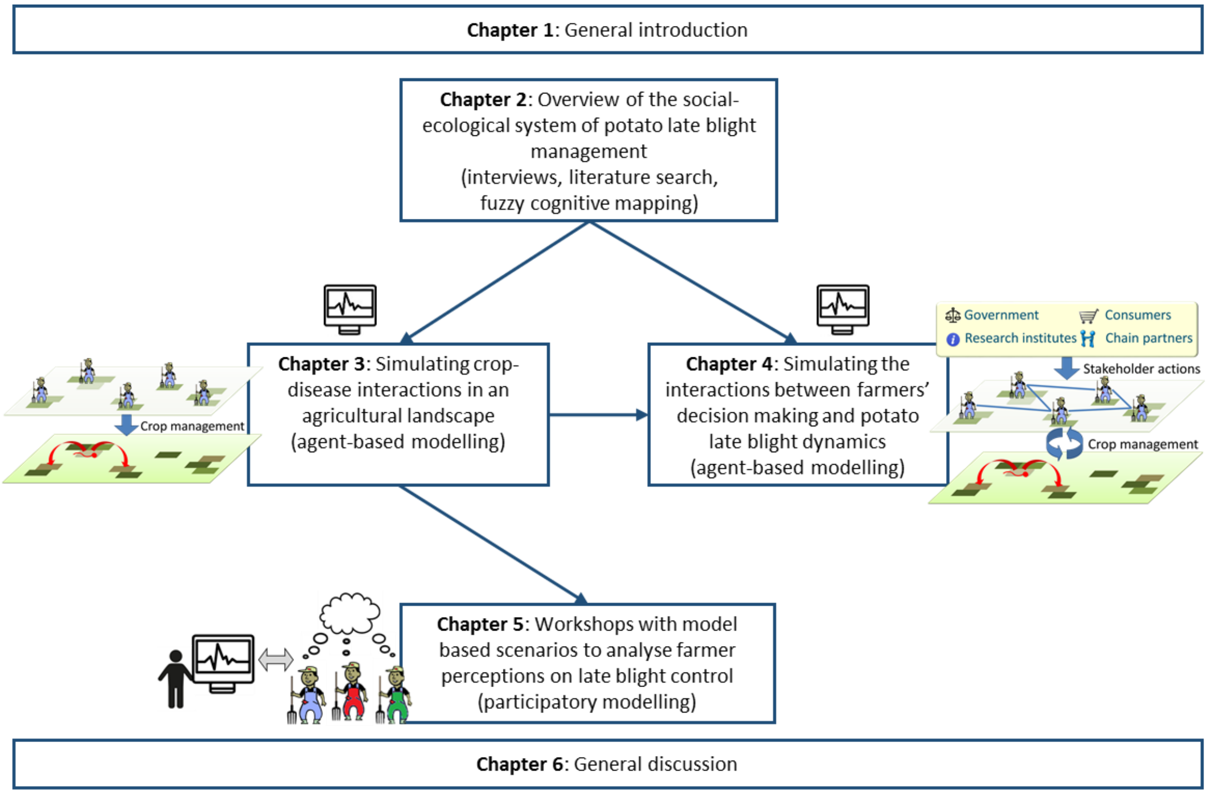

Figure 1.3. Schematic outline of the thesis. Arrows between chapters indicate that the research builds on previous work.

In Chapter 3 and 4 spatially explicit agent-based models are developed to analyse different aspects of the social-ecological system. Chapter 3 explores the use of crop resistance in disease control by simulating crop-disease interactions at the landscape level affected by weather conditions. The model is used to analyse how late blight severity, resistance durability and potato yield are affected by spatial deployment of a late blight resistant variety. The potential and risks related to the use of crop resistance in disease control are discussed.

Chapter 4 focuses on the social-ecological interactions between farmer behaviour and late blight dynamics. A framework on farmers' decision making is developed and added to the previously developed model. The factors and processes that affect the adoption of a resistant variety by farmers and resistance durability are analysed. Scenarios are analysed that represent changes in the social environment that could affect the selection of management strategies by farmers.

In Chapter 5 a modified version of the model developed in Chapter 2 is used in workshops with groups of farmers. Several scenarios are presented which show the effects of farmer management strategies regarding the use of crop resistance and fungicide application on disease control at the landscape level. A number of resistance management strategies are analysed that could increase resistance durability. The model is used as a learning tool to increase farmers' understanding on the system dynamics and to demonstrate and discuss the potential role of resistant varieties for effective and sustainable control of late blight. The workshops are organised with organic and conventional farmers to analyse their perception on late blight control.

Chapter 6 presents a discussion on the main findings of this thesis, the methodology and the implications for late blight control.

Chapter 2

Analysing potato late blight control as a social-ecological system using fuzzy cognitive mapping

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Abstract
Potato late blight, caused by *Phytophthora infestans,* is one of the main diseases in potato production, causing major losses in yield. Applying environmentally harmful fungicides is the prevailing and classical method for controlling late blight, thus contaminating food and water. There is therefore a need for innovative research approaches to produce food sustainably. Here we used a systems approach to identify sustainable management strategies for disease control in potato production in the Netherlands. We focussed not only on ecological processes, the classical approach, but also on decision-making concerning disease management. For that we performed a literature study, stakeholder interviews and modelling using fuzzy cognitive mapping. Interviews were carried out with farmers, representatives of breeding companies and experts. The fuzzy cognitive map allows to identify major concepts and their influence on late blight management. Three management scenarios were analysed using the fuzzy cognitive map. Results show that published research on the control of potato late blight focuses on agronomic practices, plant breeding for resistance to late blight and chemical-based disease suppression. Farmers are strongly influenced by corporate (such as traders, breeders and retail), and public institutes and policies, each pushing their own objectives and interests. The fuzzy cognitive map showed that social and ecological processes are tightly related. The scenario analysis showed that increasing stakeholder cooperation and a change in market demands towards resistant cultivars could improve sustainability of late blight management. In contrast, policies restricting the use of fungicides would result in increased disease severity if no alternative strategies were implemented. Adoption of such strategies would require social-institutional support and facilitation. We conclude that our systems approach improves the understanding of the system dynamics which is necessary for developing and deploying effective strategies for controlling *P. infestans*.

Keywords: *Phytophthora infestans*, cropping systems, sustainable disease management, potato production chain, socio-institutional interactions

2.1 Introduction

The Netherlands is a large producer of seed, ware and starch potatoes and therefore potato is an economically important crop (Haverkort et al., 2008). Due to the high density of potatoes and favourable weather conditions, late blight (caused by *Phytophthora infestans*) is one of the most important diseases in potato production. Infection by *P. infestans* results in foliage death and tuber rot in the field and during storage, which leads to major losses in yield. The pathogen has a short life cycle that can be completed in less than a week and potentially produces large quantities of spores. As a result of wind dispersal of the spores, and the potentially large number of generations, a late blight epidemic can spread over large regions in a short time (Zwankhuizen and Zadoks, 2002). Currently, the use of fungicides is the most important method to control blight, but this involves high costs and the fungicides are harmful for the environment (De Jong and De Snoo, 2002; Van der Werf, 1996). The environmental costs are related to the pollution of groundwater, energy costs for application and negative effects on human health (Haverkort et al., 2008). In addition, about half of all fungicides applied in the Netherlands is used for the control of potato late blight as often weekly sprayings are needed. Regarding the options in disease control a strong difference exists between organic and conventional farmers. In contrast to other European countries, the use of copper as fungicide is not permitted in the Netherlands so organic farming systems have no chemical means to combat late blight. Therefore yields can be dramatically low in years of early outbreak of late blight. To reduce the amount of fungicides in conventional systems and to improve disease control for organic farmers the development of resistant cultivars is a top priority (Finckh et al., 2006).

Late blight resistant cultivars of potato developed by commercial breeding companies can play a key role in sustainable management of potato late blight (Figure 2.1). Breeding for resistant cultivars started in the beginning of the twentieth century when the first resistant genes (R-genes) were discovered in the closely related species *Solanum demissum* (Fry, 2008). Unfortunately, when cultivars with these resistant genes came to be more widely grown, the R-genes from *S. demissum* have been broken as a result of pathogen evolution. Currently, several new resistance genes from different genetic resources are being used in classical breeding programs to develop new resistant cultivars (Lammerts van Bueren et al., 2008). Breeding for varieties with resistant genes from wild relatives is time consuming, so additional management practices are required to protect new resistance genes in cultivars from resistance breakdown.

In management of potato late blight, farmers play a key role since they make decisions on crop management. In adopting management strategies farmers are also influenced by other stakeholders such as breeding companies, traders and policy makers, who have their own objectives and interests. For example, farmers try to optimize their profits, breeding companies aim to increase their return on investment and the government facilitates sustainable food production. Farmers are also affected by the management strategies of other farmers since infections in one field can spread by wind to neighbouring uninfected potato fields. Due to high density of potato, the Dutch government has implemented a policy that regulates maximum late blight disease thresholds. At an estimated 5% infected leaf area per field, the potato haulm has to be destroyed to prevent spread to neighbouring fields (NVWA, 2008). In years with early outbreak this can cause severe yield loss and farmers tend to delay the moment of defoliation. Therefore, late blight management is also a social problem with related issues such as trust, social pressure and conflicts.

Figure 2.1. A picture showing the difference in late blight infection in susceptible and resistant potato cultivars. The susceptible cultivars in the front are almost completely destroyed by late blight while the resistant cultivars in the back are not harmed by the disease.

Overall, the disease incidence in a landscape is the result of interactions between plants and pathogens through disease epidemiology as well as stakeholder behaviour (Rebaudo and Dangles, 2012). Therefore, to identify sustainable management strategies of potato late blight, it is important to consider both biophysical and social aspects and their interactions. Also in our definition of sustainability we consider environmental, economic and social consequences of management practices, because alternative strategies that could reduce the environmental impact of disease management must also be practically and economically attractive for successful implementation (Duru et al., 2015a; Sadok et al., 2008; Thierfelder et al., 2013).

The objective of the paper is to provide an overview of the system components and their interactions, and important drivers of the system. To analyse and describe the components, the interactions and feedback mechanisms related to late blight management in the Netherlands, three different methods were used; 1) literature review on late blight management, 2) semi-structured interviews with stakeholders and 3) a modelling exercise called fuzzy cognitive mapping. With fuzzy cognitive mapping as a semi-quantitative method the main components of the system identified could be modelled (Kok, 2009). We developed three different scenarios for stakeholder management and control of late blight. The effect of the scenarios on late blight severity was analysed using the fuzzy cognitive map.

First we present an inventory of the existing research and approaches for late blight control, then we analyse the importance of the social-institutional context of potato cultivation and disease management, and last we discuss the relevance of an integrated social-ecological perspective.

2.2 Materials and methods

In this paper late blight management in the Netherlands is analysed and the system components, interactions and feedback mechanisms are identified and described. Current research on late blight management was analysed to identify important aspects in the control of late blight. A brief literature review was carried out to analyse articles related to management of potato late blight. These articles discussed several aspects that were divided into categories. The main findings for each category were described and expert knowledge was used to include relevant literature missing in the analysis.

Semi-structured interviews were carried out to identify current management strategies in the Netherlands, stakeholder objectives and factors involved in decision-making. Semi-structured interviews were carried out with representatives of breeding companies, farmers and experts. Five representatives of two of the largest Dutch breeding companies were interviewed to identify their organisational structure, marketing strategies and breeding programs in relation to resistance of potato to late blight. In total, 25 farmers were interviewed by using semi-structured interviews on topics such as general farm characteristics, their social network, problems in potato production, current late blight management strategies, and the use of late blight resistant cultivars. A stratified sample of farmers was selected based on region, farmer type (conventional/organic) and diversity in management. In total 18 conventional and 7 organic farmers were interviewed mainly from the northern part of the Netherlands. This is an important potato growing region that includes the production of seed, ware and starch potatoes. Most of the organic farmers were located in the province of Flevoland, an agricultural region with a relative large number of organic farming systems.

Both organic and conventional farmers were included since these groups differ in their options for control measures and may also differ in their decision-making and interest in disease control strategies. Based on the results from the interviews, we identified the main differences in management strategies between farmers and the drivers involved in their decision-making processes. Two experts, a researcher specialised in plant diseases and a farm consultant, both familiar with organic and conventional productions systems, were interviewed to develop a broad perspective on the issues in potato production and late blight management as well as differences in the management strategies of farmers. All interviews were recorded and transcribed for further analysis.

After the main components of the system had been identified using the results from the literature review and interviews, the system was modelled in a semi-quantitative tool called fuzzy cognitive mapping (Kok, 2009). Fuzzy cognitive mapping is a computational modelling technique that represents the main components, processes and drivers of the system (concepts) as well as their causal relationships. The relationships can be defined as positive or negative and to each relation a weighting factor is assigned. The weight quantifies the strength of the relationship between the concepts and is a number between -1 and +1. Weighting factors were divided in four groups representing weak (0.1), medium (0.25), strong (0.5) and very strong (0.75) relations with a positive or negative effect. Every simulation time step the value of the concepts will be updated by using a matrix calculation. The new state can be calculated by multiplying the state vector, which contains all the concept state values, with the adjacency matrix, including the values of all the relations between concepts. This process can be repeated indefinitely which can result in several patterns. Therefore the simulation time step represents the number of iterations of the matrix calculation. Usually it takes 20-30 iteration steps to determine the pattern. When the model output results in an equilibrium the values of the concepts in the stable state can be compared for different model settings. Fuzzy cognitive mapping is called semi-quantitative because the values of model variables can only be compared relatively to other numbers. Furthermore the iteration step cannot directly be translated to time since the processes in the model usually act on different scales.

After developing a first draft of the fuzzy cognitive map, a workshop with experts was organised to validate the map. Organising workshops with stakeholders is a common approach in the development of a fuzzy cognitive map because the model will represent a consensus of various opinions (Kok, 2009). Since the goal of the model is to get an overview of the system, the workshop with experts was used to validate the important concepts and relations. Six experts took part in the workshop with different specialisations including host-parasite interactions, plant pathology, plant breeding, agronomy, agro-industrial chains and climate change and agriculture. In general, the results from the workshop supported the initial model version but based on the workshop discussions some modifications were made to summarise similar concepts and to better represent causal relationships. To determine the contribution of a concept in a fuzzy cognitive map the centrality was calculated, which shows to what extent the concept is connected to other concepts (Özesmi and Özesmi, 2004). The centrality is calculated by the summation of its indegree (in-arrows) and outdegree (out-arrows) in which the absolute weight of all incoming and outgoing relations is summed. The indegree and outdegree can be used to determine if the concept mainly influences other concepts (a 'transmitter' with high outdegree), is mainly influenced by other concepts (a 'receiver' with high indegree), or both.

2.3 Results and discussion

2.3.1 The ecological system of potato and *P. infestans*

In the scientific literature many aspects and analyses were described related to late blight management. These research topics were divided into categories and described in the following sections. Most of the research on the potato-late blight system has been focussed on the primary characteristics of the plant and its pathogen, the host-pathogen interactions, and on the most effective measures to directly suppress the pathogen. This has resulted in many studies analysing the genetics of *P. infestans* (Section 2.3.1.1), the development and application of chemical fungicides (Section 2.3.1.2) and the late-blight resistance of potato through breeding or genetic engineering (Section 2.3.1.3). Alternative measures such as cultivar diversity and host distribution (Section 2.3.1.4), biological control (Section 2.3.1.5), and indirect strategies to build plant robustness through for instance soil fertility (Section 2.3.1.6) have been studied less. Integrated approaches that exploit the diversity of management approaches have been analysed in field experiments and models have been used to analyse those approaches in patterns in space and time (2.3.1.7). These approaches are however more complex to implement but can be supported by tools like computer-based decision support systems (Section 2.3.1.8). A separate line of research concerns the effects of environmental condition such as climate change (Section 2.3.1.9), which can potentially be relevant for the whole late blight-potato system and the effectiveness of all disease suppression approaches.

2.3.1.1 *P. infestans* population structure and diversity

The genetic research investigated the diversity and aggressiveness (virulence) of the pathogen. The plasticity of pathogenicity in the genome of *P. infestans* results in rapid adaptation and the ability to overcome both the sensitivity to fungicides and the resistance of potato plants to the disease (Goodwin et al., 1995). *P. infestans* has different mating types, called A1 and A2. For a long time after its establishment in 1845 only one mating type (A1) was present in Europe (Fry, 2008). The second mating type (A2) was probably introduced by a shipment of potatoes in 1976/1977. With both mating types present the pathogen was also able to reproduce sexually resulting in the formation of oospores, that can survive in the soil for some years (Olanya et al., 2009). New molecular diagnostic tools allowed analysis of *P. infestans* isolates to examine the genetic diversity (Cooke and Lees, 2004). These methods also allow easy determination of mating type and virulence related to resistant cultivars and fungicides. In recent years, the *P. infestans* population structure has been analysed in many countries in Europe, Asia and South America and the United States and Canada and is in some cases also being monitored over time (Harbaoui et al., 2013; Li et al., 2013). This research showed that in many potato growing regions the *P. infestans* population is dominated by a few genotypes, which can be stable for several years (Peters et al., 2014) or change rapidly over time (Cooke et al., 2012). Monitoring *P. infestans* population structure and change could be useful in making decisions on disease management with respect to cultivar selection and fungicide application. For example in the US a reduced use of fungicides was associated with the recurrence of mefenoxam sensitive strains which can have practical implications for late blight management (Hwang et al., 2014). Also, when new *P. infestans* strains emerge that are insensitive to certain fungicidal compounds or contain compatible virulence genes of certain resistant genes, countermeasures can be taken to prevent further spread of these populations. This can mean switching to other types of fungicides or to cultivars with different resistance genes till these specific traits are no longer found in the *P. infestans* population. This type of management has not yet been put into practice, but could be promising for the future.

2.3.1.2 Chemical control

The application of fungicides is currently the most important strategy in the control of late blight by farmers in the Netherlands. Several types of fungicides exists for foliar and tuber treatments. These can be contact or systemic fungicides that have a protective and/or curative effect (Gossen et al., 2014). Most research on fungicides focuses on their effectiveness against late blight but also performance related to spraying schedules and application methods have been investigated. In the Netherlands, most fungicides are used as a preventive measure. *P. infestans* strains can also become insensitive to fungicides as was found in the case of the fungicide metalaxyl (Gisi and Cohen, 1996). Insensitivity to this fungicide is now found all over the world and research was carried out to collect more information on metalaxyl resistant strains such as their mating type, aggressiveness etc.. In many countries metalaxyl is no longer used or only in combination with other fungicides. Many different fungicides exist but researchers continue to search for new active compounds (Merk et al., 2011). Fungicide manufacturers try to improve the durability of fungicides by combining active compounds. They also advise farmers to use fungicides with different modes of action over the season to reduce the risk for emergence of resistant strains.

2.3.1.3 Resistant cultivars

An important aspect in sustainable management strategies is the use of resistant cultivars. Regarding their use, many different aspects were investigated such as the mechanisms related to host defence and the identification of resistance genes

(Bengtsson et al., 2014; Rauscher et al., 2006). Breeding for resistance to late blight started a long time ago. In the classical approach wild late blight resistant potato species are crossed with modern cultivars. This introgression process is time consuming: it can take some 16-20 years before a new genitor is available for commercial breeding and multiplication. The genitors are used to develop resistant cultivars which can result in cultivar release on the market. When breeding for resistance, it is important to focus not only on foliar resistance but also evaluate tuber resistance, since these are not always correlated (Park et al., 2005). With a technique based on genetic engineering called cisgenesis or intragenesis, it is possible to introgress resistant genes from wild potato species directly into existing cultivars (Haverkort et al., 2008). This method is faster compared to classical breeding programs but this technique does not seem to work with all existing cultivars and also the long-term effect of these insertions is unknown. Because many resistant genes have been overcome by the pathogen in the past, researchers continue to search for new and more durable ones. One of the strategies emphasised is breeding for combined (stacked) resistance genes from different genetic resources, but this is even more time consuming and costly than breeding for cultivars with a single resistant gene. It is also yet unknown whether a combination of two, three or four genes is needed to prevent breakdown of resistance (Tan et al., 2010).

2.3.1.4 Cultivar diversity and host distribution

The use of resistant cultivars in the control of late blight was analysed in field experiments and simulation models. Recent research insights into the spatial epidemiology of *P. infestans* suggested that major advances in reduction of the disease could be achieved by combining traditional (chemical) methods of disease control with spatial management of resistant cultivars at field to regional scales (Skelsey et al., 2010). A spatially explicit simulation model of *P. infestans* dispersal in potato cultivar mosaics was used, which showed that an increase in the area of resistant cultivars was very effective in suppressing the spread of the disease. Mixing susceptible and resistant cultivars on small scales (at plant and row levels) was most effective in decreasing disease spread. Field experiments with intercropping systems or mixed susceptible and resistant potato cultivars often resulted in significant reductions of the disease but have not been able to eradicate it completely (Andrivon et al., 2003; Garrett and Mundt, 2000).

2.3.1.5 Biological control

The use of chemical fungicides in the control of late blight has always been under debate because of the high frequency of application and amount used in control and the negative effect they can have on the environment and to the people that work with them (Haverkort et al., 2008). This, and the fact that the application of chemical fungicides is not allowed in organic potato production, makes it of great importance to keep searching for other biological control methods such as biocontrol agents, plant extracts and biopesticides. These biological methods were applied as seed, foliar and/or tuber treatment to assess their ability to suppress late blight. Some of these compounds have been proven to be effective, however, none of them work as well as regular fungicides (Gachango et al., 2012; Olanya and Larkin, 2006; Shanthiyaa et al., 2013). However, these practices could contribute to sustainable management and therefore it has been suggested to combine these practices with other biological, cultural and fungicide approaches (Glare et al., 2012).

2.3.1.6 Soil management

Another example of an alternative strategy is soil management. Soil management, including fertilizer application, can have an effect on plant growth and physiology, which can influence host defence responses (Cicore et al., 2012). For example, in vitro studies showed that nitrogen supply increased susceptibility of potato to *P. infestans*, however, under field conditions no effect was observed. Furthermore, management strategies could affect antagonistic microorganisms in the soil that inhibit infection of *P. infestans* (Lozoya-Saldaña et al., 2006; Tamm et al., 2010). In the case of *P. infestans,* under environmental conditions oospores can survive in the soil for about three to four years and if potatoes are grown within this period initial infection as a result of the presence of residual oospores can occur (Turkensteen et al., 2000). In the Netherlands infections originating from oospores were mainly found in potato producing regions with narrow rotation schemes and therefore a bigger rotation scheme is recommended to prevent such sources of infection (Evenhuis et al., 2007).

2.3.1.7 Integrated disease management

Integrated disease management is described as a combination of methods to limit the use of chemical fungicides to a minimum (Schöber, 1992). Because many of the previous described strategies such as intercropping or fungicide application result in ineffective or unsustainable control these can be combined to improve disease management. The use of resistant cultivars is an important component in integrated disease management and it has been analysed how these can be combined with other strategies. Strategies included in integrated disease management research are for example host resistance, host density and diversity, seed tuber pre-sprouting and application of fungicides (Möller and Reents, 2007; Mundt et al., 2002). In another study also planting time was part of an integrated approach in combination with fungicide application and host resistance (Kankwatsa et al., 2002). Field experiments that combined host resistance and fungicide use showed that the disease could be controlled with less fungicides by lowering the fungicide dose or longer application intervals (Kirk et al., 2005; Nærstad et al., 2007). Integrating these two types of management strategies was already analysed by (Fry, 1977) and recently this approach was also used in combination with cisgenic resistant potatoes (Haverkort et al., 2016).

2.3.1.8 Decision support systems

Decision support systems (DSS) have been developed with the aim of optimizing the use and timing of fungicide application in order to achieve efficient spraying and to prevent fungicide insensitivity (Wharton et al., 2008). For more information on the development and availability of DSS, and the adoption and use by farmers we refer to the following two references (McCown, 2002; Shtienberg, 2013). Overall these systems use several types of information such as the crop condition and weather data such as temperature, wind speed, rainfall and humidity to estimate the risk of *P. infestans* infection and to predict outbreaks. Not all systems take cultivar resistance into account (Grünwald et al., 2000) while this is an important factor for estimating infection risk. Recently, attempts have been made to update these systems with information on spore dispersal by monitoring airborne inoculum (Fall et al., 2015). Spores can be monitored by spore sampling networks for early detection of incoming inoculum. This type of information can be used to optimize the timing of fungicide application. However, model-based analyses performed by (Skelsey et al., 2009b) showed that adding information on spore dispersal in DSS is only useful in the case of (partially) resistant cultivars. This is because the risk for infection in susceptible cultivars is high and achieving the accuracy of dispersal information required to make reliable decisions on disease management is practically unfeasible. In the case when only susceptible cultivars are grown on a field already a very low spore input resulted in yield loss, so to make decisions on disease management it is risky to rely strongly on spore dispersal information.

2.3.1.9 Effects of climatic conditions and climate change

Weather conditions constitute the most important factor influencing growth and spread of potato late blight. Optimum conditions for late blight include high humidity and a temperature of about 20°C (Crosier, 1934). Wind is responsible for the dispersal of the spores. Most of these spores will be deposited only a few meters from the initial source but dispersal across large distances can also take place. Sunlight has a negative effect on *P. infestans* since ultraviolet light will damage the spores. More information on the effect of weather variables on the developmental stages of *P. infestans* can be found in the following references (Andrade-Piedra et al., 2005; Mizubuti et al., 2000; Mizubuti and Fry, 1998).

It is well known that climate change can increase the severity of plant diseases (Gautam et al., 2013). Changes in temperature, atmospheric moisture content and CO_2 concentration can affect processes related to pathogen growth, reproduction and survival. Furthermore these factors can also affect the application and effectiveness of current management practices (Schaap et al., 2011). For example, dry weather is required for the application of fungicides. Recently, for the Dutch context new climate change scenarios of the Royal Netherlands Meteorological Institute have been published in the KNMI'14 scenarios (Van den Hurk et al., 2014) which showed minor changes in humidity for all four scenarios, the main factor influencing the establishment of the pathogen. Most scenarios even showed a decrease in humidity with a maximum of 3.0%, while only in one scenario humidity increased with 0.1%. Therefore it is not expected climate change will have a strong effect on late blight severity in the Netherlands. However, unpredicted side effects can play a role. For example, mild winters can have a positive effect on the survival of inoculum in the soil, which can lead to outbreaks early in the season (Gautam et al., 2013). Therefore the effect of climate change should be closely monitored in the future.

2.3.2 The social system of potato cultivation and late blight management

From the previous section we conclude that a diversity of management strategies exists that mainly focuses on the host-pathogen interactions and the most effective measures to directly suppress the disease. In this section we will focus on the social aspects and aim to give an overview of the Dutch potato sector with the important stakeholders and their objectives and interactions in relation to late blight management. We will start by providing a description of the Dutch potato sector that includes many stakeholders involved in different aspects of the potato production and supply chain (Section 2.3.2.1). We will describe how the market demand influences which potato types and cultivars are produced and thus how the market demand affects disease susceptibility. Secondly, we will give an overview of the stakeholders involved in late blight management (Section 2.3.2.2). Farmers play a key role since they have to make decisions on late blight management but are influenced by other stakeholders with specific objectives. We will describe differences between farmers, current management practices and the factors influencing decision-making (Section 2.3.2.3) and aim to give an overview of the most important interactions. In the last section we will show that different objectives and interests by stakeholders make it difficult to introduce new strategies in the control of late blight (Section 2.3.2.4).

2.3.2.1 Dutch potato sector

Many stakeholders are involved in the production of seed, ware and starch potatoes in the Netherlands (Table 2.1). They are involved in different aspects of the production and supply chain including cultivar availability, crop management, potato production, processing and marketing. Breeding companies are responsible for developing new potato cultivars and are usually connected to a trading company. Potatoes are grown for different markets (table, chips, fries, etc.) and each of them requires specific potato traits. Therefore, breeding companies select for many different characteristics of which late blight resistance is only one. Other characteristics include yield, nutrient requirements, shape, storage characteristics, cooking and baking quality and resistance to other pests and diseases (Tiemens-Hulscher et al., 2013). Trading companies are in

Table 2.1. Overview of stakeholders with their role in potato production and objectives, based on interviews and literature.

Stakeholder	Role in production chain	Objectives
Farmers	• Potato production • Potato management	• Maximize profit and minimize risks • Easy and sustainable potato production
Breeding companies	• Cultivar availability	• Maximize profit • Breeding potatoes with different traits to serve markets worldwide
Trading companies	• Potato marketing	• Maximize profit • Quick and wide application of new potato cultivars • Follow world-wide markets • Protect cultivars from resistance breakdown
Processing industry	• Potato processing • Potato marketing • Potato demand	• Maximize profit • Require potatoes with specific traits
Retail	• Potato marketing • Potato demand	• Maximize profit • Follow consumer preferences
Agro-Chemical industry	• Potato management	• Maximize profits • Develop and market fungicides • Prevent fungicide insensitivity
Consumers	• Potato demand	• Cheap, healthy and attractive products
Government	• Potato management	• Protect public health and the environment • Reduce late blight infection pressure
Research institutes	• Potato management	• Improve sustainability of late blight management

charge of marketing the potatoes to a variety of clients with specific market demands. Many of the seed potatoes are exported worldwide and only a part remains in the Netherlands to produce ware and starch potatoes for the industry and/or retail. In the production chain, between the trading company and the end-user, potatoes can cross several more actors involved in distribution, packaging and handling. In this system trading companies play a key role since they form a link between the market demands, the breeding companies and the farmers. They have contracts with customers worldwide as well as with the processing industry.

The variation in demand leads to a production of more than 400 different cultivars in the Netherlands (Lammerts van Bueren and Van Loon, 2011). In general, only a few cultivars are produced in large numbers while the majority of cultivars is used for niche markets. An extreme case is found in Belgium, where cultivar Bintje occupies about fifty percent of the cultivated potato area (De Blauwer and Florins, 2014). Apart from positive traits as both table and processing potato, this cultivar is also notorious for its susceptibility to many diseases including late blight. For the industry and retail, traits such as tuber and cooking quality have a high priority while the agronomic characteristics of the cultivar, including disease susceptibility, are of secondary importance. We learned from the semi-structured interviews that once supply chain parties are accustomed to certain cultivars that meet the market requirements it is hard to introduce new cultivars due to inflexibility of the supply chain. Therefore, the introduction of new cultivars is a long process and requires large investments from breeding companies. One of the interviewed experts formulated this as following: '*In the past we have seen a lot of cultivars coming and going. So if trading companies have a few cultivars that serve the market well, they don't say goodbye to these cultivars quickly when somebody is suddenly very enthusiastic about a new resistant cultivar. These new cultivars have to be introduced and well accepted by the market*.'

2.3.2.2 Potato production and management

Farmers have to make decisions on crop management but they are also influenced by other stakeholders. The agro-chemical industry is responsible for the production and distribution of fungicides. They advise farmers which fungicides to use over the season for effective control and to prevent fungicide insensitivity. This requires social organisation in which manufacturers and farm advisors play a central role. Research institutes have another objective; they aim to improve sustainability of late blight management by developing new strategies (see section 2.3.1). However, many of the strategies investigated are not (yet) commercially available (e.g. biological control), still in an early stage (e.g. late blight monitoring) or do not fit within the current production system (e.g. intercropping with resistant cultivars or other crops that are non-hosts).

Resistant cultivars could contribute to sustainable disease management. We learned from the interviews that the recently introduced late blight resistant cultivars were not attractive to all farmers as they lack some of the preferred market characteristics. For example an organic farmer stated that: '*We also tried to grow a resistant cultivar on a few hectares but at a certain moment we were not able to sell them anymore to the market.*' Furthermore, the current resistant cultivars are not as high yielding as some of the established cultivars. Therefore, the market demand for current resistant varieties is still low and because the application of fungicides leads to effective and cheap control there is no strong economic incentive to make use of late blight resistance in the conventional sector. In the organic sector the use of resistant cultivars is more promising according to stakeholders, since there is a strong need for alternative control methods. However, this sector is responsible for only ±2% of the total potato production in the Netherlands (CBS, 2016), which can be considered a small market.

Using cisgenic cultivars could potentially contribute to solving problems related to cultivar demand, since resistant genes from wild potato species could be introgressed into already established and existing cultivars that supply a large part of the market. However, the current European regulations consider this technique as genetic modification and the growth and production of these cisgenic potatoes is strictly regulated. To obtain permission to produce cisgenic potatoes a risk assessment should be carried out to ensure these crops are not harmful for the environment and human and animal health. Besides possible negative effects for the environment this topic is also under political and societal debate (Jochemsen, 2008). One of the issues is related to the intellectual property rights, also known as plant variety rights and patents (Louwaars et al., 2009). Cisgenesis is an expensive breeding tool and therefore the biotechnical industry seeks to protect their technical invention by patents. Possibly, this could have a negative effect on the breeding sector because it is not allowed to use these cultivars in breeding programs without permission of the patent owner. Examples in other crops show that as a result of patent positions only a few companies are in control of a large part of the world market which threatens innovation in plant breeding. Therefore changing the regulations regarding the production of cisgenic crops also includes institutional changes related to these products.

The Dutch government influences late blight management also in other ways. Over time policies have been introduced to reduce negative environmental impact of fungicides (Staal et al., 2014). Type and amount of active compounds are regulated for use over the years and this has reduced the pressure on the environment. As mentioned earlier the introduction of sanitary regulations by the government also helps keeping disease pressure low by mandatory rules for prevention and removal of infected sources. This includes covering cull piles and removing infection sources in potato fields as well as removing volunteers. An inspection was set up that could fine farmers in case these regulations were not followed.

2.3.2.3 Farmers

Farmers are the key stakeholder in the production and management of potatoes. In The Netherlands around 9000 farms grow potatoes on a total area of about 1500 km^2 (CBS, 2016). These farmers can be subdivided based on the type of potato they produce (seed, ware or starch potatoes) and the way of cultivation (conventional or organic).

There is a large difference in late blight management between conventional and organic farmers. For conventional farmers the application of fungicides is the most important control method, sometimes supported by the use of DSS. In contrary to other countries, in the Dutch organic sector neither the use of synthetic chemicals nor the use of copper is allowed in the control of late blight. Organic farmers are not able to control the disease but they can reduce yield loss due to infection by applying pre-sprouting of potato tubers or growing early or (partly) resistant cultivars. From the interviews we learned that in years with severe outbreaks many of the Dutch organic farmers did use copper in low doses as foliar fertilizer, which had some effect on preventing or slowing down the infection. Applying copper as fertilizer is allowed in case a low copper content is measured in the soil which is often the case in Dutch landscapes. Within the organic sector this subject is under debate. For example one organic farmer said: '*In the past we applied some copper but we rather don't use it. We are not one hundred percent against this method but we don't prefer to use it. I will only apply it in cases with extreme weather*'.

How conventional and organic farmers perceive late blight, is related to their options for disease control. For organic farmers late blight is the largest problem in potato production while conventional farmers name various other pests and diseases that cannot be treated effectively such as bacteria or nematodes. This can be supported by two statements from an organic and a conventional farmer. A conventional farmer mentioned: '*Free-living nematodes are a problem. We have to do something about that. Potato late blight has not been a problem the last years because of the large range in crop protection products we can use*'. The organic farmer has a different view: '*I am growing organic potatoes for thirty years now and I think potato late blight is the worst disease compared to all other diseases in organic agriculture. We can deal with most of the diseases but late blight gets out of control*'. So in the case of late blight, organic farmers feel they have no means to combat the disease while some other pest and diseases can be controlled by for example a broader crop rotation (in the case of nematodes) or hygienic measures. Resistant cultivars are not widely used since only a few varieties are available and the market demands are low.

The way potatoes are cultivated and managed differs for each potato type, and although there is no strict spatial segregation, there are regions where different potato types dominate. Factors related to the management of different potato types that directly affect late blight dynamics are the time of harvesting and the rotation plan. Producers of starch potato usually have a rotation plan with fewer crops (1:2 instead of 1:3 or 1:4) which results in a larger risk on initial infection as a result of oospores remaining from a previous potato crop, since these spores can survive in the soil for about three-four years (Evenhuis et al., 2007). In the starch potatoes producing area in the Netherlands it was found that the genetic variation in the *P. infestans* population was much larger than in other parts of the Netherlands as a result of oospore-driven epidemics (Li et al., 2012). The time of harvesting can affect spread of *P. infestans* since early harvesting will result in lower potato densities later in the season, which can slow down a late blight epidemic. Compared to starch and ware potatoes, seed potatoes are harvested early in the season (early July). This is also beneficial with respect to late blight since the time exposed to infection is shorter.

Farmers' decision-making is an important aspect influencing disease management. These decisions are influenced by economic incentives which includes a trade-off between reducing management costs and limiting the risk of disease damage. Infections can result in reduced yields but also in reduced quality of crop products (Lefebvre et al., 2015). The financial losses related to an infection in a potato field differs per potato production type which results in differences in late blight management. For example, in the Netherlands seed potatoes have to be certified by an authority (NAK) to be declared to be disease free. An infection in a field of seed potatoes includes a risk that these potatoes will not be certified and cannot be sold as seed potatoes, while *P. infestans* infection in starch potatoes is of less concern since they will be directly processed in a factory. Furthermore, the product price of seed potatoes is higher than for starch potatoes. Therefore, the incentive to adopt more sustainable management strategies, to reduce fungicide use and to save costs is stronger for starch potato growers compared to seed potato growers.

Based on the interviews, also other farmer characteristics were found that probably influence farmers' management strategies such as risk-perception, innovativeness, accuracy and environmental care. Furthermore, farmers in the region also influence each other and they copy each other's behaviour and thus management strategies. Farms are located in a landscape and farmers spend much time on their land so they are well aware how other farmers (successfully) manage their crops. This awareness can also lead to social conflicts in the control of late blight in case of failures to control the disease. *P. infestans* disperses by wind so infections can spread to neighbouring uninfected fields. Therefore, a lot of peer pressure exists around the control of late blight. The introduction of an anonymous hotline as part of the sanitary regulations where farmers can report an infection source, increased the tension among farmers and undermined trust, and resulted in conflicts in the neighbourhood, as was found in the interviews.

2.3.2.4 Stakeholder objectives

All stakeholders previously described have their own interests, which affect potato late blight management (Table 2.1). Conflicting interests between stakeholders are observed. For example many of the stakeholders, including farmers, are commercial entrepreneurs so their main aim is to maximize their profit. Therefore, these stakeholders follow the market demands for specific potato traits, which makes it hard to introduce (new) resistant cultivars as part of late blight control. Furthermore the agro-chemical industry aims to maximize their profit by developing and marketing fungicides while research institutes, as well as the government, try to improve sustainability of late blight management, if possible with less fungicides. Many of the strategies proposed are more time and labour demanding and are not in line with farmers' interests since this increases the management costs. For example, current potato production is based on mono-cropping and the machinery used for planting and harvesting cannot be used in intercropping systems. Also, pre-sprouting of seed-tubers or monitoring *P. infestans* populations requires extra work and an investment in equipment. These conflicting interests make it difficult to change the status quo and introduce new strategies in potato late blight management.

2.3.3 Fuzzy cognitive mapping

Based on previous findings a fuzzy cognitive map was developed. The fuzzy cognitive map shows the important concepts and their relations influencing late blight infection and management (Figure 2.2). The goal of the model is to give an overview of the system and to identify strategies and drivers that could positively affect sustainable late blight management. Not all factors mentioned in the ecological and social analysis were included since these were basically too many. Concepts (indicated in italics below) were selected based on importance and some others were combined. Important concepts were those that could have a strong effect on late blight infection and management according to the literature or the social analysis. The factors that were combined included management strategies of potato late blight because these were too many. In literature many different management strategies were described which were summarized in two concepts: *Fungicide application* and *Integrated disease management*. *Fungicide application* represents various types of chemical control while the concept *Integrated disease management* includes alternative strategies that reduce the use of fungicides. Susceptible and resistant cultivars were separately distinguished in the map since these are two main factors influencing *Late blight severity*. Groups of stakeholders were not included in the map since their relations cannot be captured in positive or negative correlations. Therefore, the social concepts were related to stakeholder objectives, interests and interactions that influence management strategies and biophysical factors.

In total 27 concepts were included in the map and 50 relations (Table 2.2). The concepts *Late blight severity*, *Integrated disease management* and *Fungicide application* had the higher scores for centrality in the map (Table 2.2). These three concepts had a relatively high indegree and outdegree, meaning that the concepts are influenced by many variables but also influence other variables themselves. These concepts are influenced by many social, biophysical and agronomic factors and their interactions. Also feedback loops are observed between biophysical and social factors. For example *Late blight severity* has a positive effect on *Concerted action* which will increase strategies related to *Integrated disease management* that reduces disease severity. Furthermore, *Environmental pollution* as a result of *Fungicide application* positively influences *Environmental awareness* that leads to *Environmental policies* aiming to reduce *Fungicide application* and *Environmental pollution*.

Six external drivers were included in the map: *Profit maximization*, *Risk-aversion*, *Farmer diversity* and *Sanitary regulations* relate to the social dimension of the system and represent stakeholders' objectives and characteristics, while *Pathogen adaptation* and *P.i. days* (the number of days per year with *P. infestans* favourable weather) are biophysical external drivers. These external drivers don’t have to be quantified because their effect is represented by the relations with other concepts.

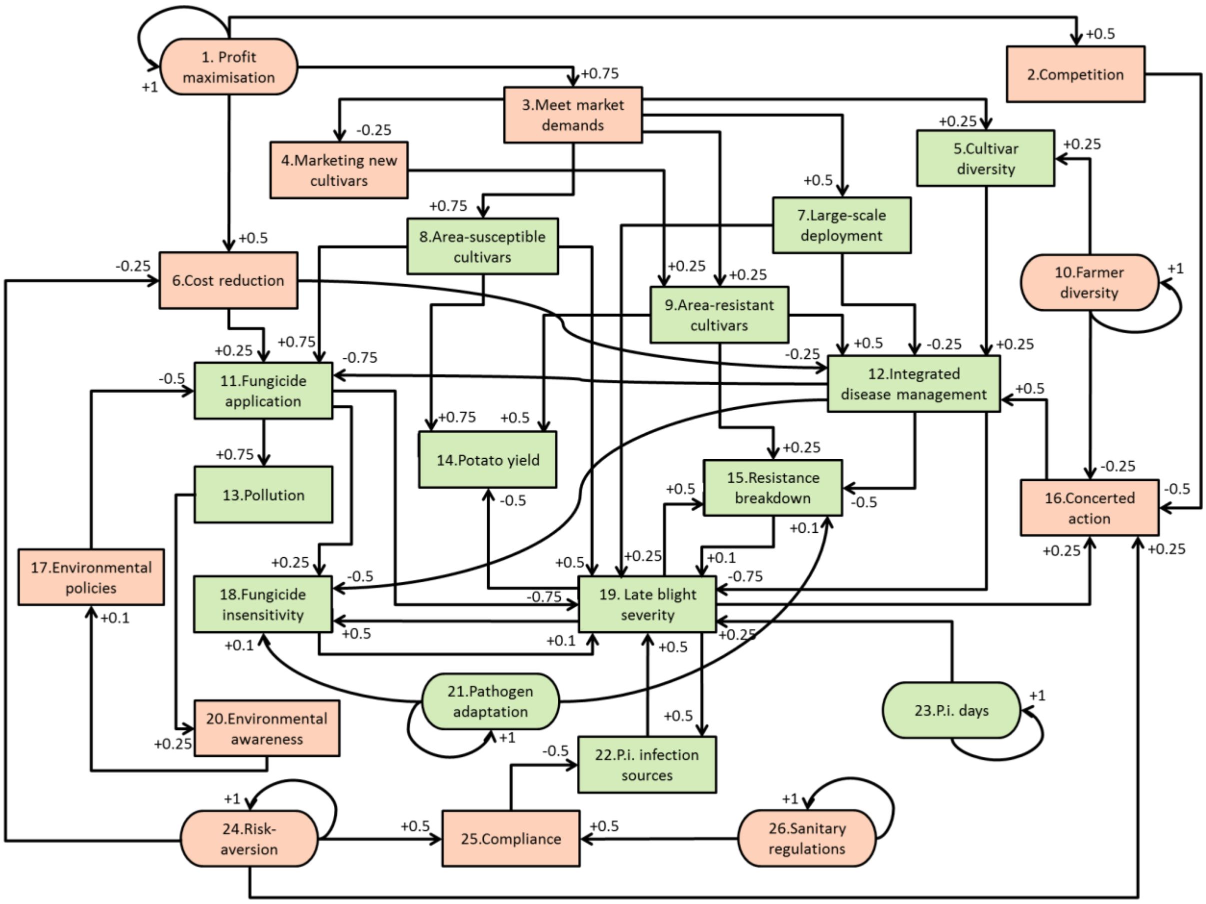

Figure 2.2. Fuzzy cognitive map of potato late blight management with the concepts and their relations *(arrows)*. *Values next to the arrows* indicate influences between concepts, which can be negative or positive (between -1 and +1). The *rounded boxes* represent external drivers of the system, *red boxes* represent social factors and *green boxes* represent biophysical/agronomic factors. *P.i.* = *Phytophthora infestans.* A description of the concepts and relations is given in Table 2.2.

Table 2.2. A description of the concepts and relations included in the fuzzy cognitive map. The numbers between brackets represent the score for centrality of each concept.

Concept	Description
1. Profit maximisation (3.75)	Within the potato production chain, many of the stakeholders, including farmers, are commercial companies that aim to maximise their profit (Table 2.1). This external driver leads not only to minimisation of costs related to late blight management but also to competition among stakeholders. Furthermore, demands of the market are followed in order to maximise potato sales.
2. Competition (1.00)	Competition among stakeholders as a result of commercial interests. For example, among farmers to produce the largest yield at low costs and sell the product at the highest price, or between trading/breeding companies to increase their market shares by releasing new cultivars. Competition among stakeholders makes it difficult to set up collective management strategies.
3. Meet market demands (2.75)	The market demands are determined by consumers but strongly influenced by (e.g.) retail and the processing and packaging industry. To maximise profit, potato cultivars are produced that meet the market demands to a large extent. Currently, the demand is high for susceptible cultivars and low for resistant cultivars. Each market requires specific potato traits which lead to a large diversity of cultivars grown in the Netherlands. However, a few cultivars supply a large part of the market, which leads to a uniform cultivation in the landscape.
4. Marketing new cultivars (0.50)	Breeding companies develop new cultivars, which have to be introduced to the market. Some of these cultivars are resistant to late blight. Due to the specific market requirements, it is hard to introduce new cultivars.
5. Cultivar diversity (0.75)	The number of different cultivars that is grown in a landscape influenced by the market demands and farmer diversity. Increasing cultivar diversity is one of the strategies that are part of integrated disease management.
6. Cost reduction (1.25)	Cultivation costs, for instance, those related to late blight management incurred for fungicides or labour. The associated costs differ between the two types of late blight management strategies included in the fuzzy cognitive map. Cost reduction has a positive effect on fungicide application since this is relatively easy and cheap, while integrated disease management is negatively affected because this is more labour and knowledge demanding.
7. Large-scale deployment (1.00)	A high density of potato and uniform cultivar selection in a landscape as a result of the market demands. A low variety of cultivars negatively affects sustainable strategies since diversity and allocation of cultivars is part of integrated disease management. Furthermore, high potato densities positively affect disease dispersal and corresponding late blight severity.
8. Area-susceptible cultivars (2.75)	The area of *P. infestans*-susceptible potato cultivars in a landscape. This is one of the main drivers of fungicide use, late blight severity and potato yield.
9. Area-resistant cultivars (1.75)	The area of *P. infestans*-resistant potato cultivars in a landscape. Resistant cultivars could play a key role in sustainable management of potato late blight and strategies for integrated disease management. However, their yield is lower than for susceptible cultivars, and when they become more widely used, the risk of resistance breakdown increases. Therefore, new resistant cultivars are developed in breeding programmes.
10. Farmer diversity (2.50)	Diversity in the farmer population with organic and conventional as the main two groups but also variation within these groups exists. This diversity leads to different cultivar preferences and a variation of cultivars in the landscape, but also makes concerted action among farmers more difficult.
11. Fungicide application (4.00)	The amount of fungicides applied for late blight control. This has a strong negative effect on late blight severity but also directly influences environmental pollution. Extensive use can lead to fungicide insensitivity of *P. infestans* .
12. Integrated disease management (4.25)	A combination of strategies to reduce the use of fungicides in late blight management such as pre-sprouting, cultivar resistance, intercropping and resistance management, which can be supported by the use of a DSS. Some of these strategies require or would benefit from cooperation among stakeholders. Integrated disease management can be very effective in late blight control and reduces late blight severity, the application of fungicides, resistance breakdown and fungicide insensitivity.
13. Pollution (1.00)	Environmental pollution as a result of fungicide application and positively affects the environmental awareness.

Table 2.2. continued

Concept	Description
14. Potato yield (1.75)	Total potato yield is influenced by the area of susceptible and resistant cultivars and late blight severity.
15. Resistance breakdown (1.45)	Breakdown of cultivar resistance to *P. infestans* as a result of pathogen adaptation. The risk for resistance breakdown is influenced by late blight severity, the area of resistant cultivars in a landscape and resistance management practices as part of integrated disease management.
16. Concerted action (1.75)	Cooperation of stakeholders in order to achieve sustainable late blight management by using integrated disease management. Competition and diversity of stakeholders negatively affects stakeholder cooperation, while an increase in late blight severity or risk-aversive behaviour increases the willingness to cooperate.
17. Environmental policies (0.60)	Policies that restrict the use of fungicides in order to reduce the negative effect of fungicides on the environment.
18. Fungicide insensitivity (1.45)	As a result of pathogen adaptation, *P. infestans* can become insensitive to fungicides. This process is positively affected by late blight severity and the use of fungicides and leads to an increase in late blight severity. Integrated disease management strategies can lower the risk on fungicide insensitivity.
19. Late blight severity (5.45)	The fraction of potato fields infected with late blight in a landscape which is affected by management strategies and epidemiological and biophysical processes. An increase of late blight severity in the landscape decreases potato yield and increases the risk for resistance breakthrough and fungicide insensitivity. An increase in severity positively affects stakeholder cooperation to switch to sustainable disease management strategies.
20. Environmental awareness (0.35)	Societal awareness about the environment as a result of environmental pollution caused by the use of fungicides. This leads to policies to protect the environment from the harmful effect of fungicides.
21. Pathogen adaptation (2.20)	*P. infestans* can adapt to the environment by mutation or sexual recombination.
22. P.i. infection sources (1.25)	*P. infestans* infection sources play an important role in outbreaks of the disease. However, late blight severity also leads to more infection sources in a landscape; so, this is a positive feedback loop. If stakeholders comply with the rules, part of these infection sources will be removed.
23. P.i. days (2.25)	The number of days with favourable weather for growth and reproduction of *P. infestans*. The weather is one of the most important drivers influencing late blight severity, and because the climatic conditions in the Netherlands are favourable for late blight, this can lead to severe outbreaks.
24. Risk-aversion (3.00)	In decisions on late blight management, risk-perception related to infection plays an important role. When stakeholders are risk-averse, they are more willing to increase management costs, take sanitary precautions and cooperate with other stakeholders in order to lower the risk for infection.
25. Compliance (1.25)	Regulations were introduced related to the removal of infection sources. When farmers do not follow these rules, they can get a fine, which positively affects stakeholder compliance. Risk-aversive behaviour also increases compliance because this will reduce the risk for infection or getting a fine.
26. Sanitary regulations (2.50)	To prevent early outbreaks of late blight, the government introduced policies related to the removal of infection sources. An inspection was set up to ensure that farmers followed these regulations.

In total three different scenarios were analysed by using the fuzzy cognitive map. These three scenarios reflect different ways in which stakeholders involved in potato production and management can influence late blight management and severity in a landscape. The first scenario is a top down approach in which the government extends the policies related to fungicide use. The second scenario shows the effect of changes in the market demands related to the selection of resistant cultivars. In the third scenario the effect of stakeholder cooperation was analysed that leads to an increase in concerted action.

An overview of the scenarios and the changes made in the model:

1) **Fungicide restrictions**: In the current fuzzy cognitive map, *Environmental awareness* as a result of *Environmental pollution* can lead to an increase in *Environmental policies* that restricts the use of fungicides. However, the positive relation between *Environment awareness* and *Environmental policies* is quite weak. In this scenario we tested the effect of introducing extra policies to further decrease the use of fungicides. This scenario can relate to an increasing concern about the harmful effect of fungicides on the environment. In the map this was achieved by adding an extra inflow of +0.5 to the concept *Environmental policies* which represents a strong effect of the introduction of new policies.
2) **Change in market demands**: As a result of profit maximization stakeholders aim to meet the market demands which currently positively affects the *Area susceptible cultivars* with a value of 0.75 and the *Area resistant cultivars* with a value of 0.25. Because markets are used to certain cultivars it is hard to introduce new ones which is visualised in the fuzzy cognitive map as a negative relation between concept 3 (*Meet market demands*) and 4 (*Marketing new cultivars*). In this scenario we analysed the effect of a change in the market demands. We assumed that the demand for resistant cultivars strongly increased and is now exactly the opposite as in the previous situation for susceptible and resistant cultivars. For example, this can be the result of an increasing interest of consumers in sustainable food products. In the new situation we also assumed the negative effect of the concept *Meet market demands* on *Marketing of new cultivars* has changed from -0.25 to +0.25 which means that new resistant varieties can enter the market.
3) **Stakeholder cooperation**: In this scenario we analysed if an increase in cooperation among stakeholders can result in more sustainable management and effective control. In the current situation *Concerted action* is inhibited by *Competition* and *Farmer diversity*. In the fuzzy cognitive map *Concerted action* contributes to *Integrated disease management* since some of the strategies require stakeholder cooperation, for example in the case of resistance management that includes spatial allocation of cultivars (susceptible and resistant cultivars, or resistant cultivars containing different resistant genes). But also strategies such as applying cultivars mixtures could benefit from cooperation of stakeholders at a larger scale. For example the possibility to sell cultivar mixtures to supermarkets would make it economically interesting for farmers to switch to alternative cropping systems. To test the effect of an increase in stakeholder cooperation an extra influx of 0.5 was added to *Concerted action*.

An overview of the results is shown in Figure 2.3. *Late blight severity* is an important indicator for the effectiveness of disease management in reducing the disease, which can be achieved by chemical control (*Fungicide application*) or a combination of more sustainable management strategies (*Integrated disease management*).

The fuzzy cognitive map for each of the scenarios evolved to a stable equilibrium (Figure 2.3), we compare in particular the relative differences in the equilibrium value of the selected concept to assess the effects of the scenario changes in the fuzzy cognitive maps. In the current situation the level of *Fungicide application* is relatively high and decreased for all three scenarios, indicating a change in

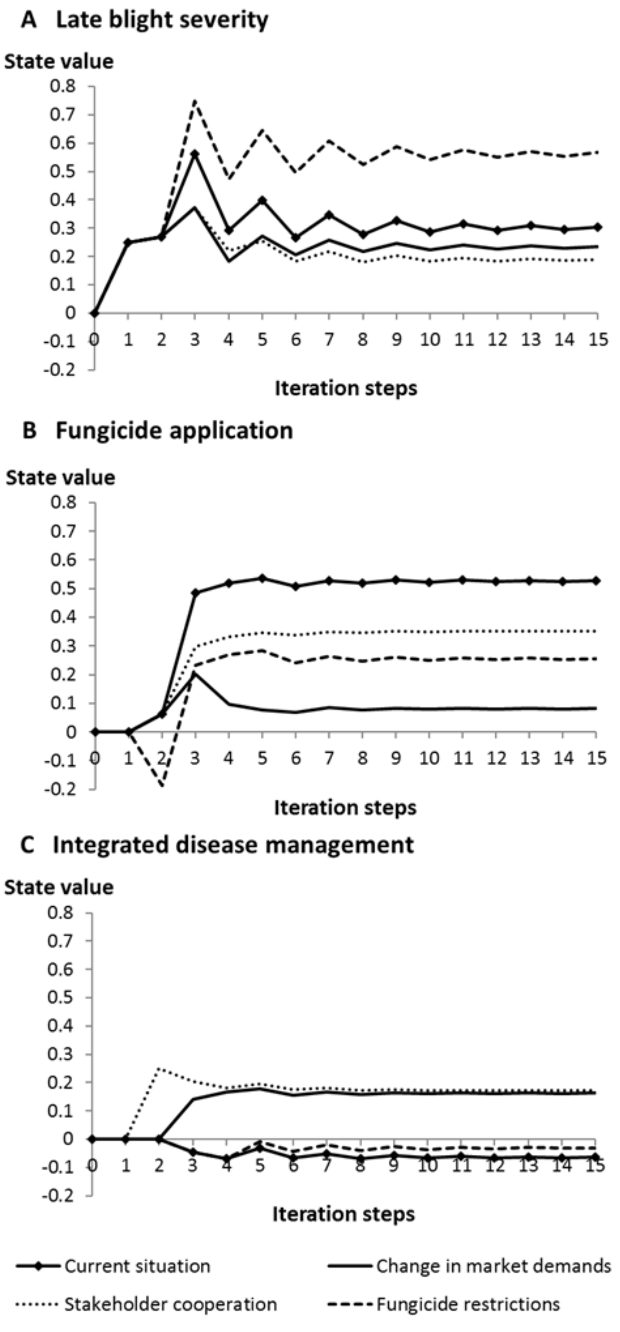

Figure 2.3. Evolution of consecutive iterations of matrix multiplications on the fuzzy cognitive maps for three concepts (A *late blight severity*, B *fungicide application* and C *integrated disease management*). The *lines* represent the values of these concepts for the current situation and three alternative scenarios (fungicide restrictions, change in market demands and stakeholder cooperation).

management practices. The scenario of fungicide restrictions leads to lower application of fungicides (Fig. 3b), but also to higher late blight severity (Fig. 3a) since integrated disease management is not increased (Fig. 3c) compared to the current situation. In contrast, a change in market demands could result in a decrease of *Late blight severity* achieved by an increase in *Integrated disease management* and a strong decrease in *Fungicide application*, which would be the most effective scenario with respect to sustainable late blight management. In the third scenario, an increase in *Concerted action* as a result of stakeholder cooperation leads to an increase in *Integrated disease management*, but the level for *Fungicide application* still remains relatively high. However, this leads to the lowest level of *Late blight severity* since *Integrated disease management* as well as *Fungicide application* is used in late blight control.

2.3.4 Synthesis

In this paper three different methods were used to analyse the components, the interactions and the feedback mechanisms related to late blight management in potato cropping systems in the Netherlands. Current literature on late blight showed that research on its control mainly focuses on agronomic practices, plant breeding for resistance to late blight and chemical-based disease suppression, and the interviews demonstrated that this reflects the most dominant approaches for disease management in practice. These approaches are effective and relatively simple and cheap to implement, support uniform cultivation practices and large-scale deployment of susceptible potato cultivars. As a consequence, they are strongly anchored in potato value chains and the current socio-technical regime (Rip and Kemp, 1998; Van der Ploeg et al., 2007). However, these traditional approaches have a negative effect on the environment and are prohibited in organic cropping systems (Haverkort et al., 2008). More sustainable and more complex strategies such as integrated disease management, cultivar resistance and spatial allocation of cultivars have also been investigated. These strategies could reduce the need for chemical control in late blight management or improve their efficiency. The literature search provided an adequate overview of management strategies, but also showed that uncertainties are involved related to responses of *P. infestans* to changes in the environment. For example knowledge is lacking on the processes that affect resistance breakdown. Another aspect contributing to uncertainty is the effect of climate change on *P. infestans* reproduction because this includes multiple scenarios whose impact is hard to predict. These uncertainties make it difficult for farmers to make reliable decisions on future management strategies of potato late blight (Duru et al., 2015b).

Besides uncertainties in ecological processes we are also dealing with a very complex social structure. The different potato value chains and the variation in the farmer population regarding potato management, contributes to the system's complexity. Many different stakeholders are involved that each have their own objectives and interests. Most stakeholders have commercial interests and aim to maximize their profits, which can result in several types of interactions such as competition or conflict but also cooperation and trading. The competition and protection of vested interests make it difficult to initialise cooperation among stakeholders to discuss the possibilities regarding sustainable late blight management (Sadok et al., 2008). In addition, decision-making is not a rational process and is influenced by many different factors such as knowledge, attitudes, goals, power and personality (Jager et al., 2000).

An assessment of sustainable potato disease management from a systems perspective requires an analysis of the social and economic viability of alternative, more environmentally benign management strategies. It is important to consider these factors since new management strategies have to be implemented in established production systems, value chains and socio-technical regimes (Duru et al., 2015a). Although technical innovations can emerge, often a description of the required socio-institutional changes for their implementation and out-scaling to system level is lacking. For example, the use of resistant cultivars could play a key role in promoting sustainable management of potato late blight. Socially this could also decrease conflicts among farmers related to late blight since the risk for infection will become smaller if many farmers would grow resistant cultivars. However, the resistant cultivars currently introduced in the Netherlands do not yet meet the requirements of farmers, the processing and packaging industry and retail. For example, desired yield level or specific cooking type are difficult requirements to meet in combination with disease resistance characteristics. Thus, production of resistant cultivars is not yet economically viable. Part of this could be solved by cooperation among stakeholders in the whole potato production chain. If a large proportion of actors would agree to move towards new type of products (e.g. resistant cultivars or cultivar mixtures) and promote these to customers and consumers, probably economic losses in the production chain could be limited by reducing transaction costs and benefit from the economies of scale. In this case resistance management strategies are required to reduce the risk of resistance breakdown. Heterogeneity in the deployment of resistance genes in space and time could improve durability but this requires planning and cooperation among breeding companies and farmers. So in order to achieve sustainable management, orchestration of management and cooperation across the whole production sector would be required (Lefebvre et al., 2015; Veldkamp et al., 2009).

The fuzzy cognitive map was developed on the basis of expert knowledge, to obtain an overview of the system components and to identify actions by stakeholders that could potentially lead to sustainable management. The fuzzy cognitive map showed that social and ecological processes are tightly related and both affect late blight severity, and allowed us to identify feedback loops, for example an increased late blight severity could lead to concerted action and more sustainable control. After years with severe outbreaks, stakeholders are probably more willing to cooperate to achieve sustainable management of late blight. Moreover, in the fuzzy cognitive map we could evaluate the potential effects of alternative policy scenarios. It was found that a top-down approach in which the government restricts the use of fungicides increased severity if no alternative strategies are implemented. The current system heavily relies on fungicide application in late blight control and the fuzzy cognitive map indicates that adoption of alternative strategies would require social-institutional support and facilitation. The other two scenarios showed the effect of increasing stakeholder cooperation and a change in market demands, respectively. Both scenarios decreased late blight severity by an increase in integrated disease management and a decrease in fungicide application, which could mean that focusing on these aspects would be more effective for improving sustainability of late blight management. The shortcomings of fuzzy cognitive maps in the analysis are the difficulty of quantifying the relative importance of the causal relationships among concepts (Kok, 2009), and the inability of fuzzy cognitive maps to represent non-linear relations, discrete events and tipping points such as resistance breakdown in the potato late blight system. In this research fuzzy cognitive mapping was mainly used in a qualitative way: to give an overview of the system and to design scenarios. The output of the model showed the changes in the system in response to several scenarios. However, the results should be interpreted with caution because of the limitations of the method. The results could serve as a basis for discussion with stakeholders to discuss possibilities for alternative management.

To represent non-linear relations other techniques like agent-based modelling (ABM) would be more suitable (An, 2012). ABM allows representing the behaviour of individuals and groups situated in a spatial environment in which biophysical processes occur, and to let the system-level patterns emerge from the actions and interactions of these components. In cases where individual components and their behaviours are more or less understood and manageable, ABM could yield policy-relevant results. As a result, ABM is a useful tool to analyse human and natural processes and their interactions (Filatova et al., 2013). Therefore a logical next step of this research would be to develop an ABM to further analyse the system dynamics.

2.4 Conclusion

On the basis of the literature review, stakeholder interviews and fuzzy cognitive map presented in this paper, we conclude that potato late blight management is an example of a social-ecological system that is driven by many processes and feedback mechanisms that interrelate and interact across multiple temporal and spatial scales. We conclude that a systems approach improves the understanding of the system dynamics which is necessary for developing and deploying effective strategies for controlling *P. infestans*. Addressing transformations toward sustainable development requires an integrated approach that allows expression of multiple perspectives on the problem, and supports an adaptive planning approach that is open for experimentation and learning (Norton, 2008; Westley et al., 2011). The analysis of such systems can be informed by multiple tools, like fuzzy cognitive mapping and agent-based modelling, which allows assessment of the complex interactions within the system and 'serious play' so that the involved stakeholders can experiment and learn. A crucial feature of these tools is that they can incorporate human responses on institutional and environmental change as affected by the implementation of new policies. Such combined modelling techniques help to understand the interactions between social and biophysical processes, which could inform discussions and negotiations among stakeholders and support learning and adaptive planning and decision-making.

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Chapter 3

Simulating crop-disease interactions in agricultural landscapes to analyse the effectiveness of host resistance in disease control: The case of potato late blight

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Abstract

Disease-resistant potato varieties can play a key role in sustainable control of potato late blight. However, when these varieties are more widely used, resistance breakdown can occur as a result of pathogen adaptation. Here we focussed on potato cultivation in the Netherlands, where new (single gene) resistant varieties have been introduced over the last ten years. This new generation of late blight resistant varieties has moderate yield levels and does not meet all market requirements. As a result, adoption rates for resistant varieties have been low so far. We developed a spatially explicit agent-based model to simulate potato production, disease spread and pathogen evolution at the landscape level. We analysed how late blight severity, resistance durability and potato yield are affected by the spatial deployment of a resistant variety, with a lower potential yield than susceptible varieties. The model was applied to an agricultural region in the Netherlands (596 km^2) and was run for a period of 36 years using daily weather data as input for crop growth and disease dynamics. The short- and long-term effects of the deployment of a resistant variety were analysed with the model. With respect to short-term dynamics, years were analysed independently to study between year variation. The model demonstrated that in most years, susceptible fields without fungicide application suffered severe yield losses and resistant fields performed better despite their lower potential yield. Infections were observed in a small fraction of fields with the resistant variety, but this did not affect mean potato yield or disease incidence in the short term since it occurred at the end of the growing season. Increasing the fraction of potato fields with the resistant variety strongly reduced late blight infection within a landscape. With respect to the long-term effects, the model showed the emergence and spread of a virulent strain over time. The virulent strain gradually took over the pathogen population, decreasing mean potato yields from fields with the resistant variety. This occurred in all landscape compositions where the resistant variety was deployed to different extents. It was found that low as well as high proportions of fields with the resistant variety could increase durability of resistance. With these findings, the model provided more insight into the opportunities and risks related to the use of plant resistance in disease control, an important and sustainable disease management strategy.

Keywords: *Phytophthora infestans,* agent-based modelling, host-pathogen interactions, cropping patterns, pathogen evolution, resistance management

3.1 Introduction

Pests and diseases can cause large yield losses in potato production and therefore, management strategies are required to secure production levels. One of the main diseases in potato is late blight caused by *Phytophthora infestans*. The application of fungicides is currently the most widely used method to control the disease, however, this involves high costs and the chemicals are harmful to the environment (Haverkort et al., 2008). One of the important strategies that could lead to more sustainable control is the use of disease-resistant potato varieties. Genes that have resistance against late blight were first discovered in the beginning of the twentieth century (Fry, 2008). When potato varieties contain these so-called major resistance genes they cannot get infected by pathogens that do not have a matching virulence gene (gene-for-gene interactions) (Flor, 1971). These genes have been used in classical breeding programs to develop resistant varieties. However, when they became more widely used, new virulent pathogen strains emerged due to pathogen adaptation which could overcome resistance (Fry, 2008). Nowadays, breeders aim to identify new resistance genes from wild relatives, which can be used to develop resistant varieties, with single or multiple resistance genes (stacking), through classical breeding or genetic engineering (Haverkort et al., 2016; Lammerts van Bueren et al., 2008). Since resistance genes are scarce and it takes large investments to develop new varieties it is important to protect new varieties from resistance breakdown.

Here we focussed on the Netherlands, which has a high potato cultivation density and a suitable climate for late blight development. In years with favourable weather for the disease (moderate temperatures and high humidity), early infection with late blight results in major yield losses in organic potato production where the use of chemicals for disease control is not allowed. Therefore, organic farmers could potentially benefit from the use of resistant potato varieties. A new generation of (single gene) resistant varieties appeared on the Dutch market in 2007. However, these new varieties have a moderate yield level and do not meet all the market requirements due to slightly different quality traits compared to those of regular (susceptible) varieties (Nuijten et al., 2017). There is currently insufficient supply of resistant seed potatoes for the entire organic market but, the sector aims to expand the production of late blight resistant varieties to completely service the organic market over the coming years (Bionext, 2017).

To analyse the effectiveness of crop resistance in late blight control we used a spatially explicit modelling approach. It is important to analyse management strategies at the landscape level because late blight is characterised by long distance dispersal and the spatial arrangement of potato crops can affect the spread of the disease (Skelsey et al., 2010) (Hossard et al., 2015; Lô-Pelzer et al., 2010). Furthermore, since evolutionary processes can take multiple years, resistance durability should be assessed over longer time periods. To analyse these spatial and temporal dynamics, modelling is a useful approach, particularly compared to field experiments which require more resources and are more constrained in space and time. The model we developed was used to simulate the effect of the spatial deployment of a resistant potato variety on late blight dynamics and potato yield.

Several modelling approaches that analyse the effect of deployment strategies on durability of disease-resistant crops can be found in the literature. These studies draw different conclusions based on the model assumptions, the outputs considered and on the host-pathogen system analysed (Fabre et al., 2012; Pink and Puddephat, 1999; Van den Bosch and Gilligan, 2003). For example, model studies differ in their assumptions as to whether costs are associated with virulence, meaning that virulent pathogens can have a reduced fitness compared to the wild-type under standard conditions (Fabre et al., 2012). Existing studies have also simulated the emergence of virulence differently, as the virulent strain can either be already present in the pathogen population (in a very small proportion), or it has to emerge as a result of mutation (Lof et al., 2017; Van den Bosch and Gilligan, 2003).

For the case of potato late blight, Skelsey et al. (2010) showed that deployment of a partially resistant variety was able to curb the spread of the disease. Partially resistant varieties slow down the epidemic in the field but cannot completely prevent infection. The most effective strategies were those that reduced the density of potato in the landscape or increased the proportion of area with the resistant potato variety (when pathogen adaptation is not taken into account).

Building on the existing research, our study focussed on the use of complete resistance (as a result of resistance genes). Specifically, we analysed how late blight severity, resistance durability and potato yield are affected by the deployment of a resistant variety. Our study is premised on several assumptions. We assume that the virulent strain has to emerge by mutations during spore production and no costs are associated with virulence. This is supported by experimental data that showed only few, or no, relations between fitness costs and virulence (Montarry et al., 2010; Schöber and Turkensteen, 1992). Secondly, it was also found that pathogenicity can rapidly evolve within clonal lineages of *P. infestans* as a result of mutation (Goodwin et al., 1995). Although the sexual life cycle of *P. infestans* also contributes to genetic diversity by the production of oospores, it was not taken into account in this study for model simplicity.

The emerging patterns of the spread of the disease at the landscape level result from interactions between spatial processes of host-pathogen dynamics and management strategies, with each acting on different temporal scales. To capture this complexity we used agent-based modelling. Agent-based models have been recognised as highly suitable for representing heterogeneous collections of interacting entities in a spatial environment in which biophysical processes occur (An, 2012). We developed submodels for late blight dynamics and crop growth and management processes as input for the agent-based model. Late blight management practices included in the model relate to current conventional and organic practices (e.g. with or without fungicide application).

3.2 Material and methods

3.2.1 Model description

The model description follows the Overview, Design concepts and Details (ODD) protocol for describing agent-based models (Grimm et al., 2006; Grimm et al., 2010). The model was implemented in NetLogo version 5.2.0 (Wilensky, 1999). A version of the model is available on the OpenABM website (http://www.openabm.org).

3.2.1.1 Purpose

The purpose of the model is to simulate the spatial dynamics of potato late blight to analyse whether resistant varieties can be used effectively for sustainable disease control. We analysed how disease severity, resistance durability and potato yield are affected by the fraction of fields across a landscape with a disease-resistant potato variety.

3.2.1.2 Entities, state variables and scales

The model comprises three hierarchical levels: grid cells, agricultural fields (cluster of grid cells) and the abiotic environment. As input for the model, data from the Noordoostpolder, a Dutch agricultural landscape, was used. The Noordoostpolder is a region of 596 km^2 with about 380 km^2 of arable land, of which 24% is used for potato production (see Figure 3.1).

The model is grid based (133 x 129 cells) and the grid cells, representing an area of 200 × 200 m^2 (4 ha), are clustered into agricultural fields. The grid cells are characterised by location, field number and crop type. Further, the grid cells with potato are also characterised by potato variety (susceptible or resistant), fungicide use and variables and parameters for crop growth and late blight infection (see Table 3.1). We consider only one type of susceptible and resistant variety (with one resistance gene). Although the yield potential may increase with the introduction of other resistant varieties, for our model we assume the resistant variety has a lower potential yield compared to the susceptible variety. This is reflected in the crop growth parameters. Grid cells belonging to the same field have the same field number, potato variety and fungicide use.

Two types of late blight are distinguished in the model: the wild-type and the virulent strain. The wild-type can only infect the susceptible variety of potato, while the virulent strain can also infect the resistant variety. At the start of the simulation only the wild-type is present. The virulent strain can emerge during the growing season as the result of mutation. When a grid cell is infected, spores are produced that are dispersed to nearby cells where they can cause infections. For more details on model processes see Section 3.2.1.3 and Section 3.2.1.7.

Since late blight development and crop growth is weather dependent, we used measured weather data from May 1 to September 30 (153 days) for 36 years (1981-2016) as model input (Section 3.2.1.3). These years represent a range of weather conditions for crop growth and late blight dynamics.

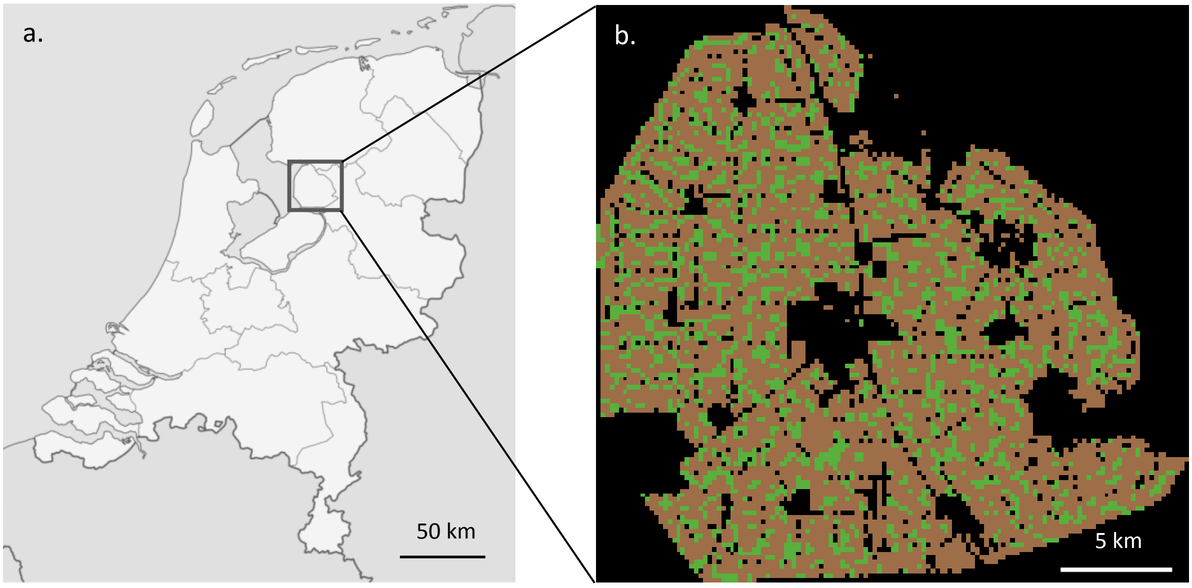

Figure 3.1. a) A map of the Netherlands with a box around the study area (Noordoostpolder), and b) the study area (grid based) which was used as input for the model (26.4 x 25.6 km^2). The black area is non-arable land (cities, water, roads etc.) or grid cells outside the study area. Brown cells represent arable land and the green cells represent potato fields. Each grid cell represents an area of 200 × 200 m^2 (4 ha) and they are clustered into agricultural fields.

Table 3.1. Overview of grid cell and global variables used to calculate crop growth and late blight infection.

Symbol	Description (unit)
Grid cell variables	
f_e	Escape fraction of the spores (-)
IE	Infection efficiency of the spores (-)
DS	Disease severity (%)
DS_v	Disease severity of the virulent strain (%)
$NLINF_v$	No longer infectious leaf tissue virulent strain (m^2)
INF_v	Infectious leaf tissue virulent strain (m^2)
$L\text{-}5_v$	Infected leaf tissue in L5 stage virulent strain (m^2)
$L\text{-}4_v$	Infected leaf tissue in L4 stage virulent strain (m^2)
$L\text{-}3_v$	Infected leaf tissue in L3 stage virulent strain (m^2)
$L\text{-}2_v$	Infected leaf tissue in L2 stage virulent strain (m^2)
$L\text{-}1_v$	Infected leaf tissue in L1 stage virulent strain (m^2)
DS_w	Disease severity of the wild-type (%)
$NLINF_w$	No longer infectious leaf tissue wild-type (m^2)
INF_w	Infectious leaf tissue wild-type (m^2)
$L\text{-}5_w$	Infected leaf tissue in L5 stage wild-type (m^2)
$L\text{-}4_w$	Infected leaf tissue in L4 stage wild-type (m^2)
$L\text{-}3_w$	Infected leaf tissue in L3 stage wild-type (m^2)
$L\text{-}2_w$	Infected leaf tissue in L2 stage wild-type (m^2)
$L\text{-}1_w$	Infected leaf tissue in L1 stage wild-type (m^2)
LAI	Leaf area index of the crop (-)
SP_v	Spore production virulent strain (no)
SP_w	Spore production wild-type (no)
Y	Potato yield (tonnes fresh matter ha^{-1})
Global variables	
Q	Daily incoming radiation (MJ m^{-2})
T	Average daily temperature (°C)
T_c	Ambient temperature (°C)
t	Time (days)

3.2.1.3 Process overview and scheduling

The time step of the model is one day and processes related to crop and disease dynamics are updated daily. We simulate the growing season from May 1 to September 30 (153 days) for 36 years. At the start of each growing season, state variables are reset and late blight infections are initialised in randomly selected potato grid cells. For every time step, meteorological data is loaded and used as input to simulate crop growth and disease dynamics. Processes impacting crop and disease dynamics are processed in the following order: 1) fungicide application, 2) calculate rates: leaf area development, tuber growth, lesion expansion and spore production, 3) spore dispersal, 4) update states: LAI, yield, lesion stages (latent, infectious and no-longer-infectious phase) and disease severity and 5) haulm destruction. For more details on model processes see Section 3.2.1.7. At the end of each year, larger scale, aggregate variables are calculated from individual cell data on potato yield and late blight infection (see Section 3.2.2). Initial model values and parameters are shown in Table 3.2.

Table 3.2. Overview of model parameters and initial model values.

Symbol	Description (unit)	Value
Crop growth		
α	Shape factor (-)	0.6
DMC	Dry matter content of potatoes (%)	25
k	Light extinction coefficient (-)	0.7
LAI_i	Initial leaf are index (-)	0.05
LAI_M	Maximum leaf are index (-)	5
LUE_s	Light use efficiency susceptible variety (kg DM MJ^{-1})	0.0010
LUE_r	Light use efficiency resistant variety (kg DM MJ^{-1})	0.0008
r_d	Relative death rate of the leaf area (°C-day^{-1})	0.010
r_g	Relative growth rate of the leaf area (°C-day^{-1})	0.015
t_e	Crop emergence (day no*)	1
t_h	Harvest date (day no*)	153
T_L	Moment of crop senescence (°C-day)	1000
T_T	Moment of tuber initiation (°C-day)	350
Late blight dynamics		
β	Shape factor	20
c_{200}	Dispersal coefficient at 200 m (-)	0.11544
c_{400}	Dispersal coefficient at 400 m (-)	0.01918
c_{600}	Dispersal coefficient at 600 m (-)	0.00691
c_{800}	Dispersal coefficient at 800 m (-)	0.00277
c_{1000}	Dispersal coefficient at 1000 m (-)	0.00125
c_f	Effect of curative fungicides on lesion growth rate of the disease (-)	0.1
DE	Deposition efficiency (-)	0.1
f_i	Fraction initial infected potato fields (infections ha^{-1})	0.02
f_m	Mutation fraction (-)	10^{-7}
f_s	Survival fraction (-)	0.2
IE_{max}	Maximum infection efficiency (-)	0.03
IE_{min}	Minimum infection efficiency (-)	0.0003
K_v	Von Kármán constant	0.35
LS_a	Area of one spore lesion (m^2)	0.0001
LS_i	Initial lesion surface area (m^2)	0.01
r_l	Lesion growth rate (day^{-1})	0.1
SI	Sporulation intensity (spores m^{-2} infected leaf area)	4.6×10^8
t_f	Fungicide application interval (days)	7
t_{50}	Time after which 50% of the fungicides is not effective anymore (days)	9
u	Mean wind speed (m s^{-1})	3
v_d	Deposition velocity (m s^{-1})	0.0255

*day no 1 = 1st of May

3.2.1.4 Design concepts

Basic principles

The representations of ecological processes were derived from a validated framework developed by Skelsey (2008) with modifications to allow for analysis of resistance durability at the landscape level.

Emergence
Late blight dynamics within the landscape emerge from the interaction between disease dispersal and distribution and management of potato fields, including fungicide application and potato variety (susceptible/resistant). Important model output at the landscape level is the fraction of infected susceptible and resistant potato fields with the wild-type and virulent strains of late blight. Potato yield is also an emergent property since it is the result of crop characteristics, late blight dynamics and the weather.

Interaction
Interaction is only modelled implicitly by spatial interactions related to disease dispersal.

Stochasticity
At the start of each simulation run management strategies (fungicide application and potato variety) are randomly divided over the potato fields. Furthermore, at the beginning of each year the infection starts in a randomly chosen fraction of potato grid cells. Last, spores are dispersed by wind and the wind direction is randomly selected (see Section 3.2.1.7).

Collectives
Potato grid cells are clustered in agricultural fields, with each field having the same fungicide use and potato variety.

Observation
Data collected from the agent-based model at the end of each growing season includes the fraction of infected potato cells (disease incidence and infected resistant fields) and potato yield. The data is collected separately for the susceptible and the resistant fields, with and without fungicide application and for infections with the wild-type and virulent strain of late blight. At the end of each year aggregate variables are calculated over the whole landscape and stored. The modelling interface presents various graphs that show the dynamics of the model outputs over time.

3.2.1.5 Initialisation
Geographical data was used as input for the model including the allocation of potato fields. Management strategies were randomly divided over the potato fields (potato variety and fungicide use). The fraction of susceptible fields with fungicide application was set at 0.90. The fraction of resistant potato fields was varied between model runs (see Section 3.2.2). Model scenarios were run using two different settings: with and without carry over effects of the virulent strain between years. In this way years were analysed independently but also in a time series to analyse resistance durability over

longer time periods. The initial values of crop growth and late blight infection are provided in Table 3.2.

3.2.1.6 Input data

Geographical data from the Noordoostpolder was used as input for the model (Figure 3.1). Crop rotation is not taken into account in the model because we don't expect crop rotation to have a strong effect on the model results. In this region farm fields are usually clustered around the homestead and the proportion of potato in the rotation is high (varying from 1:3 in conventional to 1:6 in organic farming systems). As a result, crop rotation only slightly changes the distances between potato fields. While rotation could affect the number of initial infections, this was kept constant between years since it was not relevant to compare different rotations in this case.

Measured meteorological data from the weather station Marknesse (in the Noordoostpolder) was used as input for the model (KNMI, 2016). Since data from Marknesse was incomplete before 1994, weather data from the Eelde station (±70 km from the study area), from 1981 to 1993, was used to obtain a longer time series. Mean daily temperature and total daily radiation were calculated and used as input in the submodel simulating crop growth. We used Pearson's correlation to compare the data at the two sites for the years that data from both weather stations was available (1994-2016). Data indicating days suitable for blight development (see definition of 'blight day' below) showed a correlation of r=0.77, suggesting that the weather experienced at both stations is similar.

Hourly weather data from May 1 to September 30 (the potato growing season) were analysed for the years 1981 until 2016 to determine if a day was suitable for *P. infestans* sporangia to cause an infection, i.e. a 'blight day'. We used rules that were based on the hourly temperature and relative humidity during a 24-hour period, as published by Skelsey et al. (2009a). The first rule states that an infection hour is defined as an hour where the temperature is between 5° and 27°C and, the relative humidity is greater than 90%. The second rule is related to the number of consecutive infection hours required to allow germination to reach completion in a 24 h period. Therefore, the mean temperature during consecutive infection-hours, T_{inf} (°C), is used: for $5° \leq T_{inf} \leq 10°$, 16 consecutive infection-hours are required; for $10° < T_{inf} \leq 15°$, 10 consecutive infection-hours are required; for $15° < T_{inf} \leq 20°$, 16 consecutive infection-hours are required; for $20° < T_{inf} \leq 27°$, 22 consecutive infection-hours are required; and for $T_{inf} < 5°$ and $T_{inf} > 27°$, spore germination does not occur (Skelsey et al., 2009a). The 24-hour period runs from 16:00 h to 16:00 h to ensure that the cut-off between time steps lies within the relative 'dry' period of the day. Due to lower temperatures during the night, the relative humidity is usually higher. We made some modifications to these rules. In our model, infection could also occur with lower temperatures of T_{inf} (between 5° and 10°C) and, consecutive infection hours were slightly reduced because of increased aggressiveness as a result of pathogen adaptation

(Cooke et al., 2011). If the conditions of the rules are met, new infections can occur as a result of spore germination. If the conditions are not met, the newly produced spores cannot cause infections and eventually die since we assume spores live only 24 hours. Based on this analysis, a list with favourable days for late blight development was given as input to the model.

3.2.1.7 Submodels

Below we present an overview of the model processes. An overview of variables and parameters used in this study can be found in Tables 3.1 and 3.2.

Crop growth

To simulate leaf area development we use equations for foliar development according to Richards (1959). To calculate leaf area expansion we use the leaf area index (LAI). Crop growth starts on the 1st of May (t=1) and the initial leaf area index (LAI_i) is set at 0.05 for both varieties. Leaf area expansion is simulated using thermal time accumulation (growing degree days). The change in LAI is calculated using two equations – one before the onset of senescence, which is determined by a fixed number of degree days (T_L; °C.day), and one after the onset of senescence. In both equations LAI is proportional to the mean daily temperature (T_C, with a base temperature of 2°C; $T_C = T-T_B$), the maximum leaf area (LAI_M) and a net growth rate (r_g before the onset of senescence) (Equation 3.1) or a net death rate (r_d after the onset of senescence) (Equation 3.2).

$$\frac{dL}{dt} = r_g * T_c * LAI * \left[1 - \left(\frac{LAI}{LAI_M}\right)^{\alpha}\right] \tag{3.1}$$

$$\frac{dL}{dt} = -r_d * T_c * LAI * \left[1 - \left(\frac{LAI}{LAI_M}\right)\right] \tag{3.2}$$

Tuber growth per day is calculated from tuber initiation until harvesting (Haverkort and Harris, 1987). The moment of tuber initiation is based on the number of the growing degree days (T_T). Potatoes are harvested at the end of the growing season on September 30. The tuber growth rate is calculated per hectare (tonnes of fresh matter) and is based on the leaf area index (LAI), the light use efficiency (LUE, kg DM MJ^{-1}), mean daily radiation (Q, MJ m^{-2}), disease severity (DS, % infected leaf tissue) and the constants, dry matter content (DMC) and light extinction coefficient (k) (Equation 3.3).

$$\frac{dY}{dt} = Q * LUE * \left(1 - e^{-k*LAI}\right) * \frac{100}{DMC} * \left(1 - \frac{DS*2}{100}\right) * 10 \tag{3.3}$$

With respect to crop growth processes, we assume that the resistant and susceptible potato varieties only differ in terms of their light use efficiency, resulting in a lower potential yield for the resistant variety compared to the susceptible variety. Tuber growth is reduced by the fraction of infected plant tissue multiplied by two, since an increase in latent area is assumed to cause an equal loss of non-lesion-covered leaf area (Van Oijen, 1992).

Late blight dynamics

Initial infections

At the beginning of each season the infection starts in a fraction of potato grid cells (f_i), which are randomly selected across the landscape. Random initiation is justified with field data that shows that a large number of initial infections are caused by infected seed tubers which are randomly distributed over farms (Evenhuis et al., 2007). Secondly, no evidence has been found for late blight hotspots, i.e. reoccurring initial infections in the same area over multiple years (Raatjes and Kessel, 2003). The fraction of initially infected potato fields is set at 0.02 infections ha^{-1}, which is based on 1 infection source per 200 ha in a landscape where approximately 25% of the area consists of potato fields (susceptible varieties) (Zwankhuizen et al., 1998). At the start of the simulation initial infections belong to the wild-type strain which can only develop in fields with the susceptible variety. The infection is initialised with an area of 0.01 m^2 of infected leaf tissue per grid cell (LS_i).

To analyse the population dynamics of the wild-type and virulent strains over time, between-year survival of these two strains is included. The fraction of initially infected potato fields is kept constant but the ratio between initial infections of the wild-type and virulent strains could change over time. The ratio between the total disease severity of the wild-type and virulent strains at the end of the previous growing season is used to calculate the number of initial infections of the wild-type and virulent strains in the following year. This process can be turned on and off in the model. If it is turned off all initial infections belong to the wild-type at the start of each year.

Lesion expansion

For simulating the spread of the disease we use an aged-structured population model including a latent, infectious and no-longer-infectious phase of lesions (Skelsey et al., 2010). When spores germinate the new lesions first enter a latent phase of five days after which they become infectious and produce spores. After the infectious phase (one day), lesions are added to the pool of no longer infectious tissue. Existing, but no longer infectious, lesions expand over time and produce new infectious tissue according to a lesion growth rate (r_l). New infections resulting from spore germination can only occur on 'blight days' (see Section 3.2.1.6) but the expansion of existing lesions occurs at every time step. The area of infected leaf tissue per stage of the disease is simulated for the two strains over time (Table 3.1). These variables are used to calculate the disease severity (DS), described as the percentage of infected leaf tissue per grid cell. The disease severity is calculated separately for the wild-type and virulent strains. A grid cell can get infected with the wild-type and the virulent strains at the same time and the infection processes of both strains are modelled identically and simultaneously.

Spore production

Based on the area of infectious plant tissue (INF) and the sporulation intensity (SI, spores m^{-2} of infected leaf area) a number of spores are produced per grid cell (SP) (Equation 3.4). Spore production is calculated separately for the wild-type and virulent strains.

$$\boldsymbol{SP(t) = INF(t-1) * SI} \qquad \textbf{(3.4)}$$

As explained above, virulent spores can emerge as a result of mutation during spore production of the wild-type strain in fields with the susceptible variety of potatoes (Equation 3.5).

$$\boldsymbol{SP(t)_v = SP(t)_w * f_m} \qquad \textbf{(3.5)}$$

The plasticity of pathogenicity in the genome of *P. infestans* results in rapid adaptation (Goodwin et al., 1995). However, the exact mutation rate is unknown. In other species the mutation rate (the natural mutation frequency per nucleotide) was estimated between 10^{-9} and 10^{-7} (Kondrashov and Kondrashov, 2010). Therefore, the mutation frequency (f_m) in the model was set at 10^{-7} in light of the rapid adaptation of *P. infestans*. This corresponds to a single nucleotide mutation which can overcome a single gene resistant variety. After spore dispersal and survival, the remaining viable spores can germinate and cause infection in susceptible or resistant fields.

Spore dispersal

A small fraction of the produced spores (the escape fraction, f_e) is dispersed to other grid cells where they can cause new infections. The remaining spores contribute to the disease severity in the same grid cell. The escape fraction is used to calculate the number of produced spores that escapes the canopy and are available for long distance dispersal (Skelsey et al., 2009b). This variable is negatively correlated to the leaf area index and is affected by the wind speed (Equation 3.6).

$$\boldsymbol{f_e = e^{-LAI\sqrt{\frac{v_d}{K_v * u}}}} \qquad \textbf{(3.6)}$$

Where v_d= deposition velocity and K_v=Von Kármán constant. The mean wind speed (u) is set at 3 m s^{-1}, which was the mean wind speed on 'blight days' according to the weather data.

Depending on the wind direction (selected randomly each day), spores are dispersed from one of the four sides of the infected grid cell up to a distance of 1000 m. In a sensitivity analysis, we explored the effect of wind direction on the model results. Data on wind direction was analysed (northeast 21%, southeast 14%, southwest 39% and northwest 26% on 'blight days') and implemented in the model using probabilities but this did not affect the model results.

Dispersal coefficients represent the fraction of spores arriving in grid cells according to their distance from the source. Dispersal coefficients are calculated using the Gaussian plume model (Skelsey et al., 2008; Spijkerboer et al., 2002) and are determined for distances between 100 and 900 m with 200 m intervals (length of one grid cell). It was assumed that spores have to disperse from the centre of the infected grid cell to the edge of a neighbouring cell to cause infection. Since late blight spores are dispersed by wind, they can travel over larger distances than those included in our study (Zwankhuizen et al., 1998). However, a model study by Hossard et al. (2015) showed that a characterisation of the landscape within 500 m around a resistant field was sufficient to analyse resistance durability for a wind dispersing pathogen. Therefore, we believe that a dispersal distance of 1000 m is sufficient for the purpose of our study.

After spore dispersal, the number of spores in each potato grid cell is calculated. This is the sum of spores that arrived via dispersal and spores that were produced in the cell. Only a fraction of the spores survives and is able to germinate. The number of germinating spores is affected by the infection efficiency (IE), the deposition efficiency (DE) and the spore survival fraction (f_s). When one or more spores germinate, these spores enter the latent phase (L-1) and the corresponding area of infected leaf tissue is calculated using the average lesion size (LS_a). The processes related to spore dispersal only occur on 'blight days', since favourable weather is required for the germination of newly produced spores.

Fungicide application

Protective fungicides are used on a fraction of fields with the susceptible variety for disease control which reduces the infection efficiency (IE) of the spores (Skelsey et al., 2009b). Fungicides are applied at weekly intervals starting on the day of crop emergence. The infection efficiency is described as the fraction of spores present that are able to infect the host. When fungicides are applied, the infection efficiency is reduced to 1% of the original value meaning that 99% of the spores are eliminated. During the days following application, the fungicides gradually degrade and the infection efficiency increases again. The infection efficiency is calculated with Equation 3.7.

$$\boldsymbol{IE = IE_{min} + \frac{IE_{max} - IE_{min}}{1 + [t_{50}/(t - t_a)]^{\beta}}} \quad \textbf{(3.7)}$$

Where IE_{min}=minimum infection efficiency (directly after fungicide application), IE_{max}=maximum infection efficiency (without fungicide application), t_{50}= the time at which 50% of the fungicides are ineffective (set at 9 days), t=time (day of the year), t_a=day of last application, β=shape factor which is negatively correlated with the time needed to reach IE_{max}.

When the disease severity in a grid cell exceeds 1%, it is assumed that curative fungicides are applied which have a similar effect on infection efficiency as protective fungicides, and in addition reduce the expansion of existing lesions by a factor of 0.1 (c_f).

Haulm destruction

When the total disease severity in potato grid cells reaches 5%, the potato haulm is destroyed according to Dutch governmental regulations (NVWA, 2008). In these grid cells, leaf and tuber growth stops directly and the disease can no longer disperse to other fields. Since disease severity per grid cell is limited to 5%, competition for space was not included in the model.

3.2.2 Model simulation scenarios

The model was used to analyse several scenarios. We used a baseline scenario with a fraction of 0.9 susceptible fields, 0.1 resistant fields and 0.9 of the susceptible fields receiving fungicide applications. This roughly represents the current situation in the case study region, which has a small number of organic farmers who do not apply fungicides and a small number of farmers growing a resistant potato variety. The baseline scenario was used for detailed analysis of host-pathogen interactions within and between years, with a particular focus on the influence of weather conditions.

Secondly, we explored the effect of the deployment of the resistant variety on disease control by adjusting the fraction of resistant fields composing the landscape (referred to as landscape composition). The fraction of resistant fields was varied between 0.00 and 0.95 with intervals of 0.10 (using a value of 0.95 instead of 1.00). For all landscape compositions, model runs were executed twice: years were analysed independently (without carry over effects between years) but also in a time series to analyse resistance durability over longer time periods. In this way, short and long-term effects of the deployment of potato varieties were compared. For each scenario, simulation runs were repeated 10 times.

We analysed potato yield and variables related to late blight infection. The following output variables were calculated from individual grid cell data: 1) potato yield; 2) disease incidence: the percentage of infected potato grid cells with a disease severity ≥ 1% (Skelsey et al., 2010); 3) infected resistant fields: the percentage of resistant potato grid cells in the landscape infected with the virulent strain; 4) establishment risk: the mean risk of establishment of the virulent strain due to between year survival (%) (therefore we analysed the percentage of years that the virulent strain emerged and survived the winter resulting in initial infections in the following year), and; 5) take-over time: the number of years it takes after establishment until 90% of the total disease severity is caused by the virulent strain.

3.2.3 Sensitivity analysis

To identify the parameters which have a strong effect on the model output, a local sensitivity analysis was carried out (Hamby, 1994; Ten Broeke et al., 2016). Most of the parameter values were derived from literature and those with large uncertainties were included in a sensitivity analysis using the baseline scenario (Table 3.3). These parameters included initial parameter values and some of the parameters related to crop growth and late blight dynamics. Parameter values were varied individually by 20% above or below their reference values (Table 3.3) and simulation runs were repeated 10 times.

3.3 Results

3.3.1 Short-term dynamics: weather variability, late blight severity and impact

The percentage of 'blight days' between May and September for the period between 1981 and 2016 is presented in Figure 3.2. Blight days as well as the relative humidity seemed to decrease over time. A multiple regression analysis with daily mean relative humidity and temperature as independent variables showed that these variables could explain 75.6% (P<0.001) and 2.8% (P<0.05) of the variation in 'blight days', respectively.

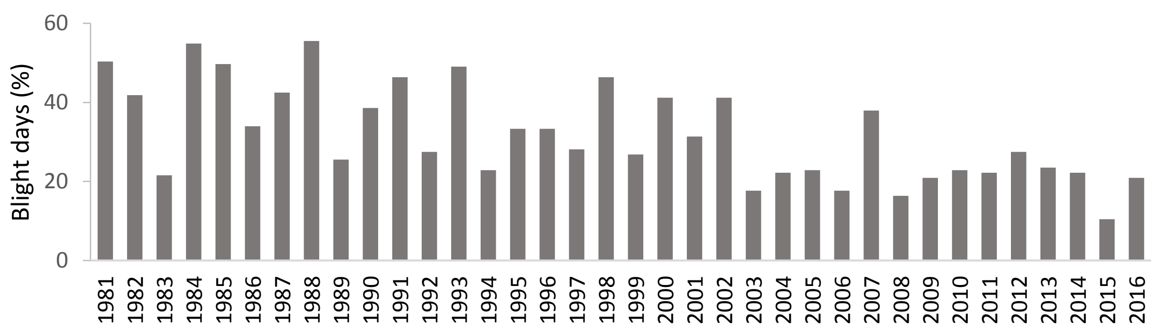

Figure 3.2. Percentage of 'blight days' between May 1 and September 30 for consecutive years in the period 1981 to 2016.

The 36 years of data simulated with the baseline scenario showed that disease incidence and potato yield varied between years and were affected by the number of 'blight days' (Figure 3.3). Each year was analysed independently, showing the host-pathogen dynamics within a season. The mean disease incidence per year ranged between 15% and 55% and increased with more 'blight days'. There was only small variation between model runs showing that the disease incidence is mainly affected by the number of 'blight days'. Due to the fixed number of initial infection sources a minimum late blight incidence was observed. Although most fields are protected by fungicides, the large fraction of susceptible potato fields in the landscape resulted in high levels of disease incidence in some of the years.

In the baseline scenario resistance breakdown occurred and the percentage of infected resistant fields (grid cells) was variable. Overall, we observed an increase in the number of infected resistant fields in the years with a larger number of 'blight days' (Figure 3.3b). The mean percentage of infected resistant fields in a year reached a maximum of 8.4% (±7.2 SD), indicating that only parts of the resistant fields were infected with the virulent strain. Resistant fields were infected late in the season. The mean day of the year that the first infections in resistant fields were reported was day 95 (±22 SD) (August 3) and, the earliest reporting was on day 50 (June 19). In many years resistant fields were not infected or the percentage of infected resistant fields was very low, even in years with a high percentage of 'blight days'. On the other hand, infections in resistant fields were observed in years with a low percentage of 'blight days'. Moreover, large variation in the percentage of infected resistant fields was observed between model runs. The variability between years and model runs showed the random nature of the emergence and spread of the virulent strain. Resistance breakdown can occur in years with high and low late blight incidence and, it is affected by random processes such as the allocation of potato varieties across the landscape and initial infection sources.

Potato yields are shown in Figure 3.3c. In general, susceptible fields with fungicide application had higher potato yields than resistant fields and susceptible fields without fungicides. Potato yields in fungicide treated susceptible fields were relatively stable between years, indicating that fungicides effectively suppress the disease within a field. In years with low infection pressure the susceptible fields, both with and without fungicides, performed better than the resistant fields. This was as expected given the assumption in the model that the resistant variety has a potentially lower yield than the susceptible variety. With the increasing number of 'blight days' resistant fields reached higher yield levels compared to the susceptible fields without fungicides, showing a strong effect of late blight infection on yield loss in untreated susceptible fields. A small decrease in mean potato yield was observed in both resistant fields and susceptible fields treated with fungicides with an increasing percentage of 'blight days'. This was largely the result of a negative correlation between 'blight days' and temperature and radiation influencing crop growth (Pearson correlation; blight days and temperature: b= -0.387 and p=0.020, blight days and radiation: b= -0.791 and p<0.001). We also observed small yield losses due to late blight infection in these fields. When we only consider the short-term dynamics, the effect of resistance breakdown on mean potato yield was low because of the low level of infected resistant fields and its late moment of occurrence in the season.

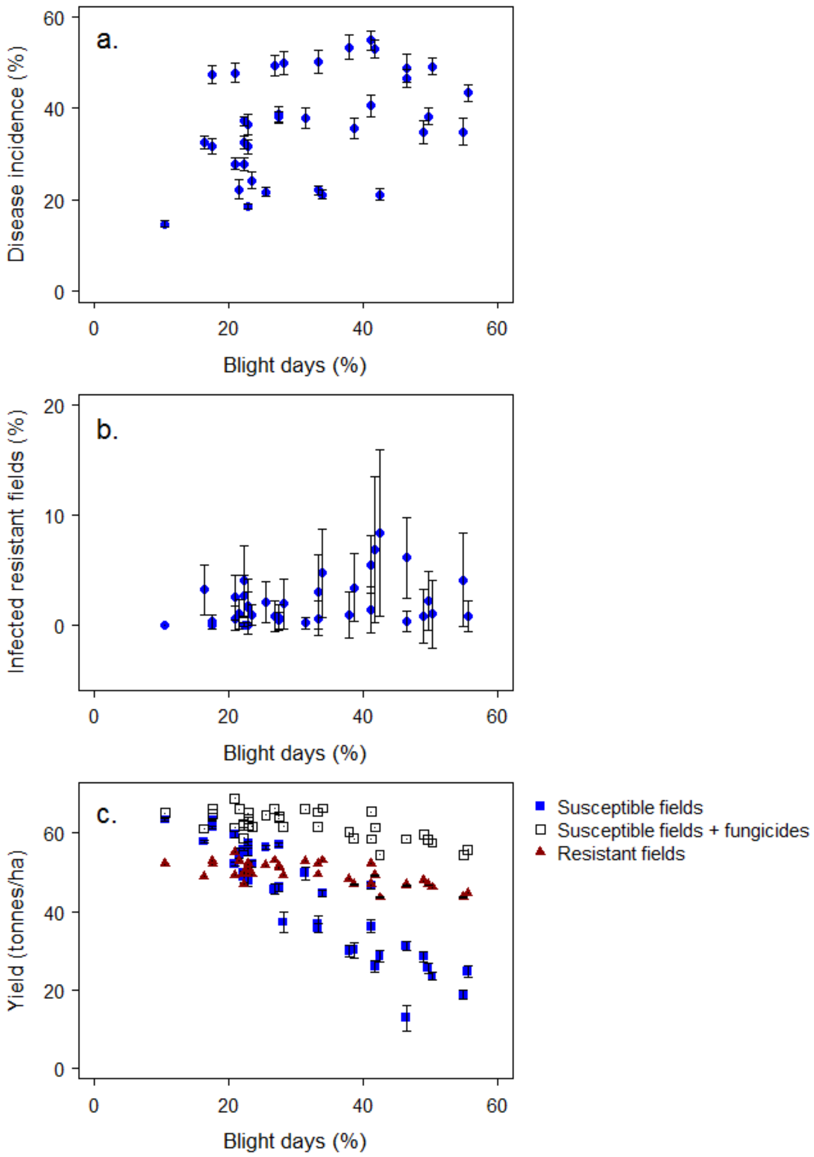

Figure 3.3. Model results for the baseline scenario (fraction of potato fields with the resistant variety: 0.1, and fraction of susceptible fields applying fungicides: 0.9) in relation to the percentage of 'blight days' (May until September for 36 years). Years were analysed independently so no carry over effects between years were included. a) Disease incidence (the percentage of infected potato grid cells with a disease severity ≥ 1%); b) Infected resistant fields (the percentage of resistant potato grid cells infected with the virulent strain) and; c) Fresh tuber yield of potato fields. The numbers represent mean values (±SD) of 10 runs.

The model showed that an increasing proportion of resistant fields resulted in a strong decrease in disease incidence across the landscape (Figure 3.4). Years were analysed independently and mean values were calculated over 36 years. Given that infections mainly occur in susceptible fields, the variation in disease incidence between years decreased with larger fractions of resistant fields (Figure 3.4a). This result also shows that random processes, including the spatial allocation of initial infection sources and potato varieties, have a strong effect on disease dispersal in susceptible fields and differ between years and model runs. The disease incidence in susceptible fields without fungicides strongly decreased when the fraction of resistant fields in the landscape was larger than 0.50 (Figure 3.4b). A larger fraction of resistant fields in the landscape reduced the number of sites where initial infections could develop at the start of the growing season (mean values of 183 and 9 initial infection sources with a fraction of 0.00 and 0.95 resistant fields, respectively). Secondly, during the season the potato fields with the resistant variety acted as a barrier for disease dispersal, preventing infection in susceptible potato fields.

The decrease in disease incidence also resulted in reduced yield losses in susceptible fields without fungicide application (Figure 3.4c), while no effect was observed on potato yields of resistant fields or susceptible fields with fungicide application.

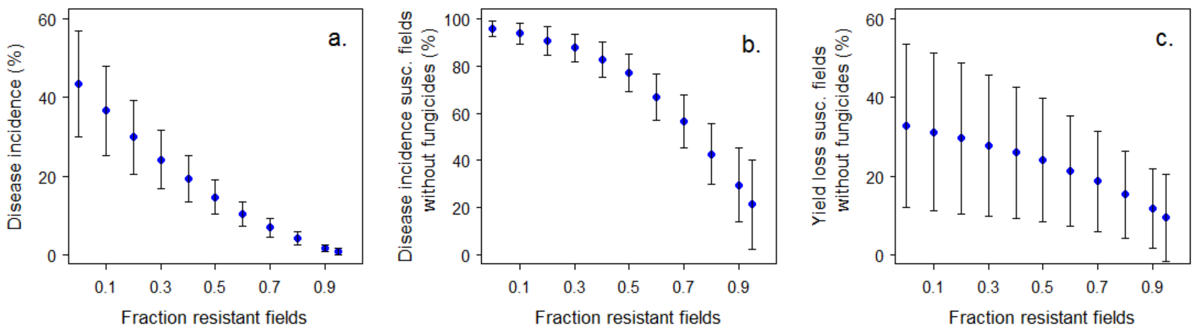

Figure 3.4. Incidence of late blight infection and yield loss in relation to the fraction of potato fields with the resistant variety (fraction resistant fields). The disease incidence (the percentage of grid cells with a disease severity >1%) is shown for: (a) all potato grid cells and; (b) the susceptible fields without fungicide application. The relative yield loss (%) for susceptible fields without fungicide application is shown in (c). Note the different scales on the Y-axes. The results show mean values and SD for 36 years of 10 model runs.

3.3.2 Long-term dynamics: pathogen evolution and durability of resistance

Figure 3.5 shows an example of the model results for long-term dynamics simulated with the baseline scenario. The simulation results of disease dynamics over longer periods show that, in the baseline scenario after some years (2 to 8) resistant fields were infected and the virulent strain gradually took over the late blight population (Figure 3.5a). The virulent strain has an advantage since it can infect both the resistant and susceptible fields while the wild-type can only infect the susceptible fields. Establishment of the virulent strain over time also resulted in increased levels of infected resistant fields and, in turn, yield losses (Figure 3.5b). The yield of the resistant fields eventually dropped below that of the susceptible fields without fungicides. when all resistant fields got infected with the virulent strain.

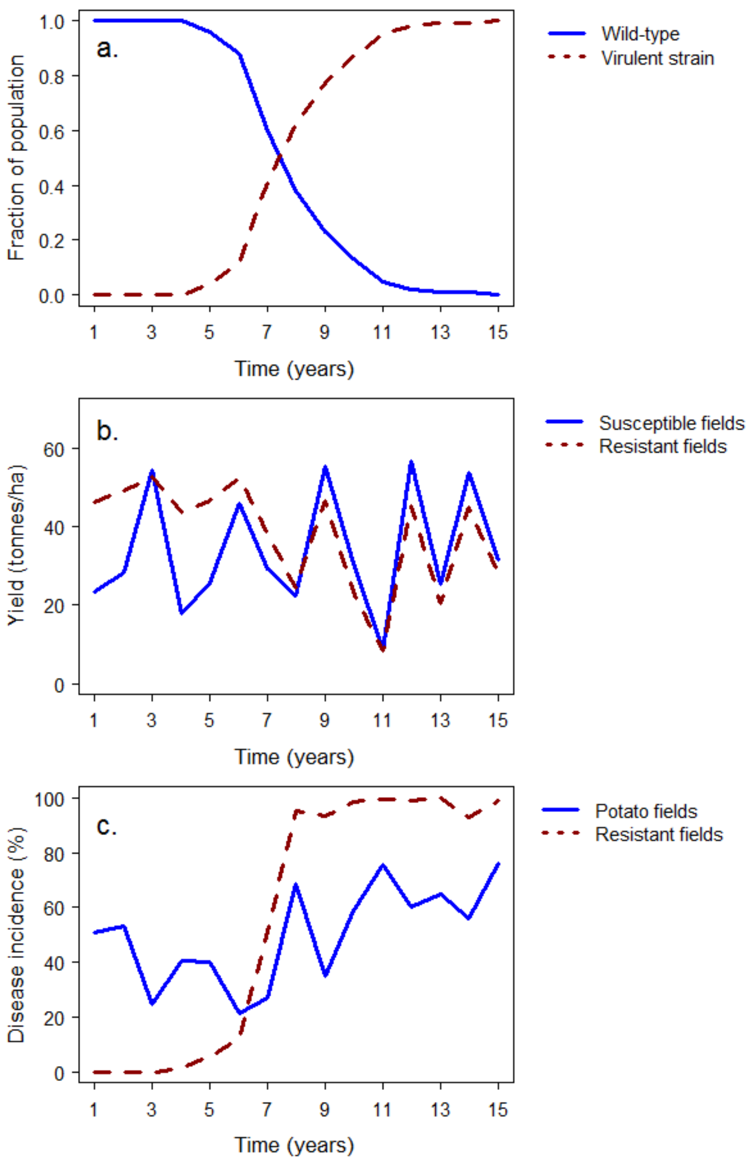

Figure 3.5. Long-term dynamics for one model run of the baseline scenario showing the establishment of the virulent strain: a) The proportion of disease severity caused by infection with the wild-type (solid line) and virulent strain (dashed line); b) Potato yield of fields with the resistant variety (dashed line) and the susceptible variety without fungicide application (solid line) and; c) Disease incidence in the landscape (percentage of grid cells with a disease severity >1%) of all potato fields (solid line) and resistant fields (dashed line).

Establishment of the virulent strain occurred in all landscape compositions where the resistant variety was grown but deployment strategies of potato varieties does influence resistance durability. Increasing the fraction of resistant fields from 0.1 to 0.5 increased the risk of establishment of the virulent strain (Figure 3.6a). With more resistant potato fields in the landscape there is an increased risk that virulent spores, emerging from susceptible fields, can spread to fields of the resistant variety, resulting in more rapid spread of the virulent strain. When the fraction of resistant fields increased beyond 0.5, the risk of establishment decreased again, probably as a result of the reduced infection pressure.

Once the virulent strain survives the winter, it gradually takes over the pathogen population. The take-over time is relatively short and decreases rapidly with increasing fractions of resistant fields (Figure 3.6b). The virulent strain has two major advantages compared to the wild-type: firstly, it can infect both the resistant and susceptible varieties and secondly, it can spread quickly through the resistant fields since we assume that these fields are not protected by fungicides.

When considering establishment risk and take-over time together, we found that with a small fraction of resistant fields there was a small risk of establishment of the virulent strain and it took more time to take over the pathogen population. On the other hand, with a large fraction of resistant fields, the establishment risk of the virulent strain is even smaller, but once establishment occurs it takes a short time to take over the population. Therefore, low as well as high cropping ratios of resistant fields can increase resistance durability.

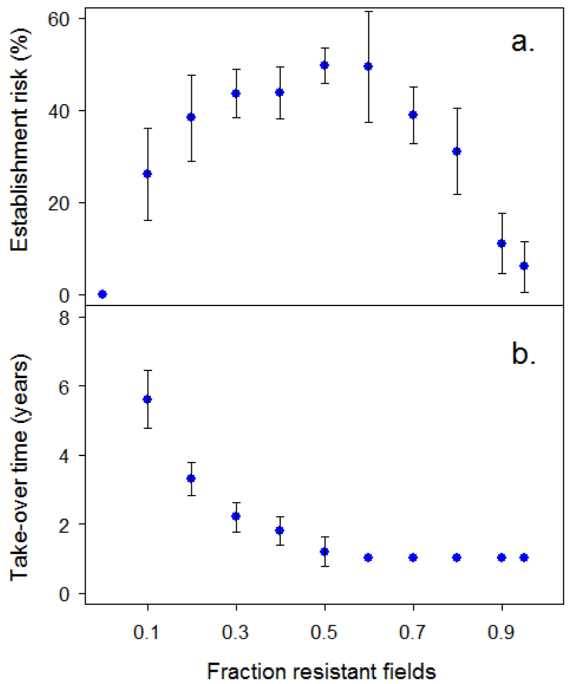

Figure 3.6. Resistance durability in relation to the fraction of potato fields with the resistant variety (fraction resistant fields). a) Establishment risk (the risk per year of establishment of the virulent strain due to between-year survival) and; b) take-over time (the number of years it takes after establishment until 90% of the total disease severity is caused by the virulent strain). The numbers represent mean values (±SD) of 10 model runs.

3.3.3 Sensitivity analysis

The results of the sensitivity analysis show the effects of varying individual parameters on the model output in the baseline scenario (Table 3.3). The effect on model output is presented as the percentage of change related to the reference value. Varying the parameters had small effects on simulated potato yields, with the exception of those directly related to crop growth such as light use efficiency. The parameters related to late blight only influenced mean yield of susceptible fields without fungicides to a maximum value of 5%.

Simulated disease incidence was affected by potato late blight parameters where changing the lesion growth rate of late blight (r_l) showed the strongest effect. Varying the leaf area growth and death rates also had a strong effect on the disease incidence since leaf area development influences disease severity at the field level (percentage of infected leaf tissue).

The percentage of infected resistant fields and establishment risk were affected by up to 45% when varying parameters related to spore dispersal and survival. In contrast, no strong effects were observed on the take-over time. It was found that increased aggressiveness of the pathogen related to sporulation intensity, infection efficiency, spore survival and mutation reduced the take-over time of the virulent strain. However, the effects were rather small (max ±15%) and inconsistent, probably due to the variation in this output variable.

3.4 Discussion

The model showed the short- and long-term effects of the deployment of a late blight resistant potato variety. With respect to short-term effects, increasing the fraction of resistant fields strongly decreased the disease incidence in a landscape. This was the result of the decreasing number of initial infection sources that can only develop in susceptible fields. After a certain threshold was reached, resistant fields acted as barriers preventing spread to neighbouring fields. Resistance breakdown was observed, late in the season, in a small fraction of resistant fields per year, and therefore did not have a strong effect on the mean potato yield of resistant fields or disease incidence in the short-term.

In the model we assumed that the resistant potato variety had a lower potential yield compared to the susceptible variety. With respect to potato yields , in many years resistant fields performed better than susceptible fields not protected by fungicides, due to yield losses by late blight infection. This demonstrated that resistant varieties can be very effective in the control of potato late blight and growing these varieties would help organic farmers to achieve acceptable yield levels. Conventional farmers could also benefit from the use of resistant varieties when economic and environmental costs related to fungicide application are considered. Furthermore, it is

Table 3.3. Sensitivity analysis for the baseline scenario, including parameters on crop growth and late blight development. Output is presented as the percentage of change related to the reference value and the numbers represent mean values from 10 model runs.

		Sensitivity (%)						
		Short-term dynamics					Long-term dynamics	
Parameter (description, reference value)	Parameter alternation (%)	Yield susc. variety	Yield susc. variety + fungicides	Yield res. variety	Disease incidence	Infected resistant fields	Establishment risk	Takeover time
Reference output in baseline scenario (mean ±SD)		43.1 ±13.9	61.9 ±3.6	49.6 ±2.9	36.6 ±11.3	2.1 ±3.3	26.1 ±9.9	5.6 ±0.8
Initial model values								
f_i (fraction initial infected potato fields, 0.02)	-20	3.9	0.0	0.0	-12.3	9.5	-6.5	-8.9
	+20	-3.2	0.0	0.0	6.8	0.0	6.5	-3.6
LAI_i (initial leaf area index, 0.05)	-20	-0.7	-1.3	-1.4	2.5	0.0	0.0	-3.6
	+20	1.2	1.1	1.0	-5.5	-9.5	-5.4	1.8
LS_i (initial lesion surface, 0.01)	-20	1.6	0.0	0.0	-6.3	-28.6	-24.5	-8.9
	+20	-0.7	0.0	0.0	1.9	4.8	22.2	1.8
Model parameters								
c_f (effect of curative fungicides, 0.1)	-20	0.5	0.0	0.0	-2.7	-14.3	-20.3	5.4
	+20	0.5	0.0	0.0	-0.5	4.8	7.7	-3.6
c_x (dispersal coefficients)	-20	1.2	0.0	0.0	-8.7	-47.6	-42.5	-5.4
	+20	0.0	0.0	0.0	2.7	14.3	9.6	-5.4
DE (deposition efficiency, 0.1)	-20	5.2	0.1	0.0	-12.2	-38.4	-31.9	5.4
	+20	-3.6	0.0	-0.1	8.7	44.1	36.2	-5.4
f_m (mutation fraction, 10^{-7})	-20	0.0	0.0	0.0	-0.8	-33.3	-33.0	5.4
	+20	0.2	0.0	0.0	-1.9	14.3	6.5	-8.9
f_s (survival fraction, 0.1)	-20	5.3	0.0	0.0	-12.6	-28.6	-37.2	0.0
	+20	-3.7	0.0	0.0	7.7	23.8	26.8	-10.7
IE (infection efficiency, 0.03)	-20	4.9	0.0	0.0	-11.5	-19.0	-26.4	1.8
	+20	-4.2	0.0	0.0	8.2	4.8	17.2	-16.1
LAI_m (maximum leaf area index, 5)	-20	-4.9	-3.9	-3.8	6.6	4.8	25.7	0.0
	+20	3.5	2.3	2.2	-9.0	-33.3	-37.2	-1.8
$LUE_{s/r}$ (light use efficiency)	-20	-20.0	-20.0	-20.0	-1.8	-3.7	-7.4	-1.8
	+20	20.0	20.1	20.0	-0.7	2.6	-5.3	-1.8
LS_a (area of one spore lesion, 10^{-4})	-20	4.9	0.0	0.0	-10.4	0.0	-14.9	-5.4
	+20	-3.7	0.0	0.0	6.8	0.0	9.6	-14.3
r_d (leaf area death rate, 0.010)	-20	3.2	7.4	7.2	-41.8	-4.2	-19.1	-5.4
	+20	-2.6	-6.3	-6.4	45.2	-12.2	7.5	0.0
r_g (leaf area growth rate, 0.015)	-20	-9.4	-14.3	-14.3	47.7	-28.1	-5.3	-3.6
	+20	5.7	10.2	10.1	-40.7	-4.1	-20.2	-14.3
r_l (lesion growth rate, 0.1)	-20	6.5	0.2	0.0	-35.0	9.5	17.2	-3.6
	+20	-4.4	-0.2	0.0	35.8	9.5	7.7	3.6
SI (sporulation intensity, 4.6 x 10^8)	-20	5.6	0.0	0.0	-13.4	-38.1	-35.2	7.1
	+20	-3.5	0.0	0.0	6.3	9.5	23.4	-7.1
u (mean wind speed, 3)	-20	0.2	0.0	0.0	-5.2	-33.3	-30.7	-3.6
	+20	0.5	0.0	0.0	0.5	28.6	7.7	1.8

expected that the yield potential will increase with the introduction of new resistant varieties, which will make them more attractive to farmers.

considered. Furthermore, it is expected that the yield potential will increase with the introduction of new resistant varieties, which will make them more attractive to farmers. Organic farmers growing susceptible varieties could also benefit from resistant varieties, since this reduces the infection pressure in the landscape leading to higher yield on fields that are not treated with fungicides. However, susceptible fields can also act as sources of infection, leading to the emergence of virulent strains and resistance breakdown over the longer term. These results show the potential benefits of growing a resistant variety but also the risk of resistance breakdown.

When analysing the long-term effects of deploying a resistant variety across a landscape the model showed resistance breakdown by the emergence and spread of a virulent strain. Mean potato yields of resistant fields decreased over time when no countermeasures were taken. This occurred in all landscape compositions but durability of resistance could be increased by maintaining either low (< 0.2) or high (> 0.8) fractions of resistant fields.

In the Netherlands new (single-gene) resistant varieties were introduced to the market in 2007 (Nuijten et al., 2017). These were mainly developed for the organic sector which is currently responsible for 1% of the total Dutch potato production (CBS, 2016). The proportion of organic production is slightly higher in this case study area with approximately 9% of the arable land in the province being used for organic farming. After a severe late blight epidemic in 2016, stakeholders in the organic potato supply chain (including breeding companies, farmers' organisations and retail) agreed to upscale the use of late blight resistant varieties (Bionext, 2017) which could also lead to an increase in organic potato production. According to the model results, the risk of establishment of a virulent strain increases when larger proportions of fields are cultivated with a resistant variety (with the same resistance gene). An implication of these results is that in the scaling up phase of using a resistant variety, breeding companies and farmers must be aware of the risk of resistance breakdown. The model showed that resistance breakdown can occur in years with low as well high disease incidence meaning that the risk is ever present. Additional management strategies are needed to prevent resistance breakdown and spread of the new virulent strain.

Several resistance management strategies have been proposed in the literature to increase resistance durability such as spatial and temporal allocation of resistant varieties with different sources of resistance genes, combining resistance genes in one variety (gene stacking) and combining resistant varieties with (reduced) application of fungicides (Mundt, 2014; Van den Bosch and Gilligan, 2003). Furthermore, the results from our study suggest that the use of early potato varieties, that can be harvested early in the season, could decrease the risk of resistance breakdown since this was mainly observed at the end of the growing season. Secondly, destroying the haulm immediately after an infection in the resistant variety could prevent spread and establishment of the virulent strain. Model studies can be used to analyse the effectiveness of these additional resistance management strategies at the landscape level (Lof et al., 2017; Van den Bosch and Gilligan, 2003).

For the implementation of such resistance management strategies concerted effort among stakeholders is required. In a previous analysis on potato late blight it was concluded that control of potato late blight is influenced by both social and ecological factors as well as their interactions (Chapter 2). Farmers play a key role since they make decisions on crop management, but they are strongly influenced by other stakeholders such as traders, breeders and policy makers, each pushing their own objectives and interests. Our model framework also allows the implementation of decision-making processes to analyse social-ecological interactions, and this will be carried out as a next step in this research.

Unfortunately, no data was available on late blight dynamics at the landscape level over time to validate the model results. The model can be described as a so-called mid-range model: the aim is neither to exactly model the situation in a certain region, nor to make a purely theoretical point (Gilbert, 2008). Therefore, it was used to identify trends rather than making predictions for the future. Although no time- or space-specific data for this, or other, case studies are available to validate the model, the trends observed in the model output can be supported by previous findings on late blight dynamics and other modelling studies. Since yield-limiting factors other than late blight infection were not included in the model, simulated yields are higher than the actual potato yields of farmers (CBS, 2016; Lammerts van Bueren et al., 2008). On average, potato yields in organic potato production are 30%-50% lower than yields in conventional production (Tamm et al., 2004). The model showed similar trends when comparing simulated yields of susceptible fields with and without fungicide application. Secondly, previous model estimations by Skelsey et al. (2010) showed that increasing the fraction of fields with a resistant variety strongly reduced disease incidence, following similar trends found in our study. With respect to resistance durability, the model showed the emergence of the virulent strain that resulted in resistance breakdown after some years. This process, whereby the virulent strain is able to establish in the population and make resistance less effective each year, has also been observed several times after the introduction of single-gene resistant varieties (Fry, 2008).

The model showed that high (>0.8) as well as low (<0.2) fractions of resistant fields could increase the resistance durability of a resistant variety. In practice, the conventional approach is to introduce low fractions of resistant varieties to the potato cultivation area since this can reduce the selection pressure on the pathogen population (Pink and Puddephat, 1999). However, these studies assume that the virulent strain is already present in the pathogen population and, after the introduction of the resistant variety, this population can rapidly increase. Van den Bosch and Gilligan (2003) showed that resistance durability can be increased by low and high cropping proportions of the resistant variety. They used similar assumptions as in our study; no fitness costs are involved related to resistance and the virulent strain must emerge by mutations in the asexual life cycle. They used several measures for resistance durability and showed that the time after which the virulent strain appears in the population (comparable to the establishment risk in our study) can be extended by small as well as large fractions of resistant fields in the landscape. Secondly, as in our study, they reported that the time until the virulent genotype takes over the population would decrease with larger fractions of the resistant variety (Van den Bosch and Gilligan, 2003). In agreement with previous literature our results also show that it is important to look at different measures to analyse resistance durability.

Theories that describe interactions between spatial diversity and dispersal can be used to explain the observed patterns related to disease severity, resistance breakdown and the fraction of resistant hosts. The Janzen-Connell hypothesis shows that interactions between hosts and pathogens shape the composition and density of species in the landscape (Gilbert, 2002). In addition, the dispersal-scaling hypothesis states that dispersal is affected by habitat size and dispersal distance, where an increase in habitat size is described as a 'positive dispersal force' and an increase in dispersal distance as a 'negative dispersal force' (Skelsey et al., 2013). These two competing forces result in a pattern where dispersal is maximised at intermediate scales. Our modelling results show that increasing the fraction of resistant fields (until a certain point) leads to a higher risk of infection with the virulent strain. With higher fractions of resistant fields virulent spores have an increased chance of arriving in these fields. However, when the fraction of resistant fields increases, the fraction of susceptible fields goes down. Since these fields host the wild-type strain, this reduces disease severity (Figure 3.4a). Given that the virulent spores are the result of mutations in the wild-type population, the risk of emergence of virulent spores decreases with a lower fraction of susceptible fields. These trade-offs result in the pattern observed in Figure 3.6b which shows the highest risk of establishment of the virulent strain occurs with about equal proportions of susceptible and resistant fields in the landscape. Once the virulent strain has established it will take over the pathogen population, and this process goes faster with larger fractions of resistant fields (Figure 3.6b).

To analyse the effect of weather variability on late blight dynamics the number of 'blight days' was calculated and used as input for the model. This parameter represents the potentially suitable conditions for late blight development during the season. Overall a decreasing trend in the percentage of 'blight days' was observed over the modelled years as a result of decreasing humidity, which is possibly the result of climate change. Despite the relatively low numbers of 'blight days' in the last decade, early and severe late blight epidemics were still observed in the Netherlands. In 2007, 2012 and 2016 infections with late blight resulted in major losses to yield in organic potato production (Knuivers, 2016; Lammerts van Bueren et al., 2008). This can partly be explained by the fact that potato late blight strains became more aggressive as a result of sexual reproduction (Cooke et al., 2011). Increased aggressiveness of the pathogen was observed by shorter life cycles, a greater temperature range, a shorter infection period, more leaf spots per life cycle and the occurrence of stem lesions (Cooke et al., 2011). In the Netherlands, for a long time, only one mating type was present, but after the introduction of the second type around 1980, the pathogen is also able to reproduce sexually (Drenth, 1994). This led to a diverse pathogen population with an increased adaptability to its host and environment. It is therefore likely that *P. infestans* will be able to adapt to new conditions as a result of climate change in the future (Van den Hurk et al., 2014). Although changes in pathogen aggressiveness were not included in the model, the sensitivity analysis shows that parameter values on late blight development can have a strong effect on disease incidence at the landscape level. Overall, the model framework has proven very suitable to analyse host-pathogen interactions within a landscape as influenced by management strategies and scenarios of environmental change, including climate change.

3.5 Conclusion

In this paper we developed a spatially explicit agent-based model to analyse the effect of the deployment of a resistant potato variety on late blight severity, resistance durability and potato yield. The model showed that in the short-term growing a resistant variety can be beneficial. In many years potato yields of the resistant variety was higher than that of the susceptible variety not protected by fungicides. Increasing the fraction of potato fields with the resistant variety strongly reduced late blight infection within a landscape, but additional management strategies are required to prevent resistance breakdown and establishment of a new virulent late blight population. The model showed that low (< 0.2) as well as high (> 0.8) fractions of fields across the landscape with a resistant potato variety could increase resistance durability. These findings provide greater insight into the opportunities and risks related to the use of resistance in disease control.

The model can be used to evaluate newly proposed sustainable disease management strategies. The results are comparable to findings from existing model studies on resistance durability of other host-pathogen systems. We developed a model that explores host-pathogen processes for the case of potato late blight in a landscape in the Netherlands., however, the model can be easily adapted to simulate other case studies.

Despite the risk of resistance breakdown, plant breeders and researchers continue to search for new resistance genes to tackle crop disease. New molecular techniques make it easier to introgress and combine resistance genes in new or existing varieties (by classical breeding or genetic engineering), which makes modelling studies, such as this, very relevant to allow ex-ante assessment of these changes.

Acknowledgements

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Chapter 4

Analysing social-ecological interactions in disease control: An agent-based model on farmers' decision making and potato late blight dynamics

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Submitted

Abstract

In agriculture damage due to pests and diseases is one of the main factors responsible for yield loss. Since disease incidence in the landscape is influenced by spatial biophysical processes as well as crop management strategies, it is important to focus not only on epidemiological processes but also on decision-making concerning disease management. Farmers play a key role since their management strategies affect disease dispersal in the landscape, but they also respond to changes in the socio-institutional and biophysical environment. In this paper we focus on potato late blight control in the Netherlands to analyse the social-ecological interactions between farmer behaviour and disease dynamics. Currently the use of fungicides is the most important control method but these are harmful for the environment. The use of resistant varieties could improve sustainability of late blight management; however, as a result of pathogen adaptation new virulent strains can emerge resulting in resistance breakdown. To analyse the interactions and feedback mechanisms related to farmers' decision making and disease dynamics we used an agent-based model. The model represents an agricultural landscape with farmers managing potato fields. The framework on farmers' decision-making was based on the Consumat approach (a well-founded theory on human behaviour) and supported by data from literature and interviews with Dutch potato farmers. This framework was integrated with a previously developed spatially explicit model on potato late blight dynamics. We assumed a scenario where a new resistant potato variety was introduced to the market. Furthermore we explored the effect of (alternative parameter values related to) fungicide costs, and crop yield and crop price of the resistant variety on the selection of management strategies by farmers and consequently, resistance durability. The model reproduced a so-called boom-and-bust cycle: the percentage of farmers growing the resistant variety increased (boom) until resistance breakdown occurred by emergence and spread of a virulent strain, and in response farmers switched to other potato varieties and management strategies (bust). Higher fungicide costs and higher yield or crop price of the resistant variety increased the adoption of the resistant variety. However, also a large number of farmers continued growing the susceptible variety with fungicides which suggests that cooperation in the whole potato sector is needed to achieve structural transformations in disease control. In addition, the high risk on resistance breakdown stresses the importance of resistance management strategies to increase resistance durability. We conclude that this approach could be useful for a whole range of systems focusing on management of emerging infectious diseases of crops.

Keywords: Social-ecological systems, *Phytophthora infestans*

4.1 Introduction

One of the main challenges in global food production is to control upcoming pests and diseases (Mack et al., 2000). Examples of emerging infectious diseases of crops include Banana Xanthomonas wilt and wheat rust (Vurro et al., 2010). These diseases can have huge impacts on human well-being, economy and biodiversity. Control of the disease is the result of an interplay between pathogens, hosts and actors. The actors in the system can have divergent approaches in disease control as a result of different perspectives and objectives. In this paper we focus on potato late blight control to analyse interactions between farmer behaviour and disease dynamics. *Phytophthora infestans*, the causal agent of late blight, first arrived in Europe in 1845 where it was responsible for the Irish potato famine in which one million people died and another one million people emigrated. *P. infestans* has a high evolutionary potential and as new strains evolve also new outbreaks of the disease emerge causing devastating epidemics globally (Anderson et al., 2004). In this project we focus on the Netherlands which is a large producer of seed, ware and starch potatoes (Haverkort et al., 2008). The high potato density and favourable weather conditions for the disease (moderate temperatures and high humidity) result in frequent outbreaks of the disease. Currently the use of fungicides is the most important control method but these are harmful for the environment. The use of resistant varieties could improve sustainability of late blight management; however, as a result of pathogen adaptation new virulent strains can emerge resulting in resistance breakdown.

Previously we described late blight management in potato production as a social-ecological system which is driven by interrelated social and biophysical processes that interact across multiple temporal and spatial scales (Chapter 2). Since the disease incidence in the landscape is influenced by biophysical processes as well as crop management strategies, it is important to focus not only on epidemiological processes but also on decision-making concerning disease management. In this system farmers play a key role since they decide on crop management. Their management strategies affect the disease pressure in a landscape and the sustainability in terms of environmental pollution and breakdown of disease-resistance, which can be considered as a common good. Secondly, farmers also respond to conditions, influences and changes in the socio-institutional setting (e.g., policies, markets, extension and peer-to-peer communication) and the biophysical environment (e.g., soil and weather), and they adapt their management strategies based on past experiences. Therefore, to identify effective and sustainable late blight management strategies, it is important to consider the social-ecological interactions.

In a previous study, we developed a model to analyse the interactions between late blight management strategies, disease dynamics and the abiotic environment at landscape level (Chapter 3). The model was used to show opportunities and risks related to the use of plant resistance in disease control. Growing a resistant variety can reduce disease incidence in the landscape; however, in the long run resistance breakdown was observed by emergence of a new virulent strain due to pathogen adaptation. The durability of resistance was affected by the fraction of resistant fields in the landscape and it was found that low (<0.2) as well as high (>0.8) proportions of resistant fields could increase resistance durability. According to the dispersal-scaling hypothesis disease dispersal is affected by habitat size and dispersal distance (Skelsey et al., 2013). A larger fraction of resistant fields results in a lower disease incidence in the landscape and reduces the risk that virulent spores emerge. However, with higher fractions of resistant fields virulent spores also have an increased chance of arriving in these fields. As a result, the risk on infections in resistant fields is highest with about equal proportions of susceptible and resistant fields in the landscape.

In this paper we focus on the social-ecological interactions by adding the dimension of decision making by multiple, interacting farmers in a landscape. To analyse the interactions and feedback mechanisms related to farmers' decision making on late blight control we used an agent-based model. Agent-based models have been recognized as a useful tool to analyse human decision-making in a spatial environment in which biophysical processes occur (An, 2012). Agent-based models consist of heterogeneous entities which interact with each other and the environment and is therefore very suitable for simulating individual decision-making agents.

During the last decades, the number of studies using agent-based modelling to couple social and natural systems has rapidly increased. Reviews on the use of models in social-ecological systems research are provided by An (2012), Filatova et al. (2013), Matthews et al. (2007), Parker et al. (2003) and Schlüter et al. (2012). One of the challenges that was identified includes the integrating of social and ecological systems (Parker et al., 2008). The number of models that is able to simulate two-way feedbacks between human and environmental subsystems are scarce while this is essential for studying non-linear interactions between human and natural systems (Filatova et al., 2016). In this study we aim to contribute to this field of research by developing a model framework which integrates farmer behaviour and disease dynamics.

To simulate human behaviour, several methods have been used. When data on decision making is scarce or missing, theories can be used and the implications can be confronted with empirical data (Groeneveld et al., 2017). The most common theory to simulate human behaviour is to assume rational decision making, also referred to as the *homo economicus* (Groeneveld et al., 2017; Schlüter et al., 2017). According to this theory agents have perfect knowledge and make calculations to identify the optimal decision that maximizes their utility or profit. However, studies on farmer behaviour have shown that farmers are also influenced by many other factors such as peer networks, individual preferences and culture (Austin et al., 1998; Edwards-Jones, 2006; Willock et al., 1999).

In our study we used the Consumat approach to simulate farmers' decision making on late blight management (Jager and Janssen, 2012; Jager et al., 2000; Janssen and Jager, 2001). The framework was first developed to explore consumer behaviour, but is now widely used in many fields of research including farmers' decision making (Malawska and Topping, 2016; Speelman, 2014; Van Duinen et al., 2016). The Consumat approach incorporates aspects from a range of behavioural theories such as theories on human needs, motivational processes, social comparison theory, social learning theory and reasoned action theory. According to the Consumat approach agents engage in different behavioural strategies dependent on their level of satisfaction and uncertainty. These behavioural strategies are repetition, imitation, optimization and social comparison (Figure 4.1). The advantage of the Consumat approach is that it is a highly formalized theory which allows easy implementation in an agent-based model and only few assumptions have to be made.

The framework was combined with the previously developed ecological model to simulate the use of crop resistance in disease control by analysing the adoption of the resistant variety by farmers and the durability of resistance over time. Therefore, we assumed a scenario in which a new resistant variety is introduced to the market. The purpose of the model is to explore the social-ecological interactions to identify factors that could be important in the development of sustainable disease management strategies. We explored several scenarios that could affect the selection of management strategies by farmers and consequently, resistance durability. In the following sections we present a more detailed description of the model, the scenario analysis and the results. In the discussion we evaluate the model findings, the implications for disease management and steps for further research.

4.2 Material and methods

An agent-based model was developed to simulate processes on crop growth, disease dynamics and farmer interactions and decision-making on disease management in an agricultural landscape over time. The model was implemented in NetLogo version 5.2.0 (Wilensky, 1999). Below we present an overview of the model with a description of the main model processes. A detailed description of the model following the ODD protocol (Overview, Design, Details) can be found in Appendix 4.A (Grimm et al., 2006; Grimm et al., 2010). For detailed information on the epidemiological framework, we refer to Chapter 3. The framework on farmers' decision-making was based on the Consumat approach (Jager and Janssen, 2012; Jager et al., 2000; Janssen and Jager, 2001) and supported by data from literature and interviews with Dutch potato farmers. In total 25 farmers were interviewed including 18 conventional and 7 organic farmers (Chapter 2). Semi-structured interviews were carried out on topics such as general farm characteristics, the social network, late blight management strategies and the use of late blight resistant varieties.

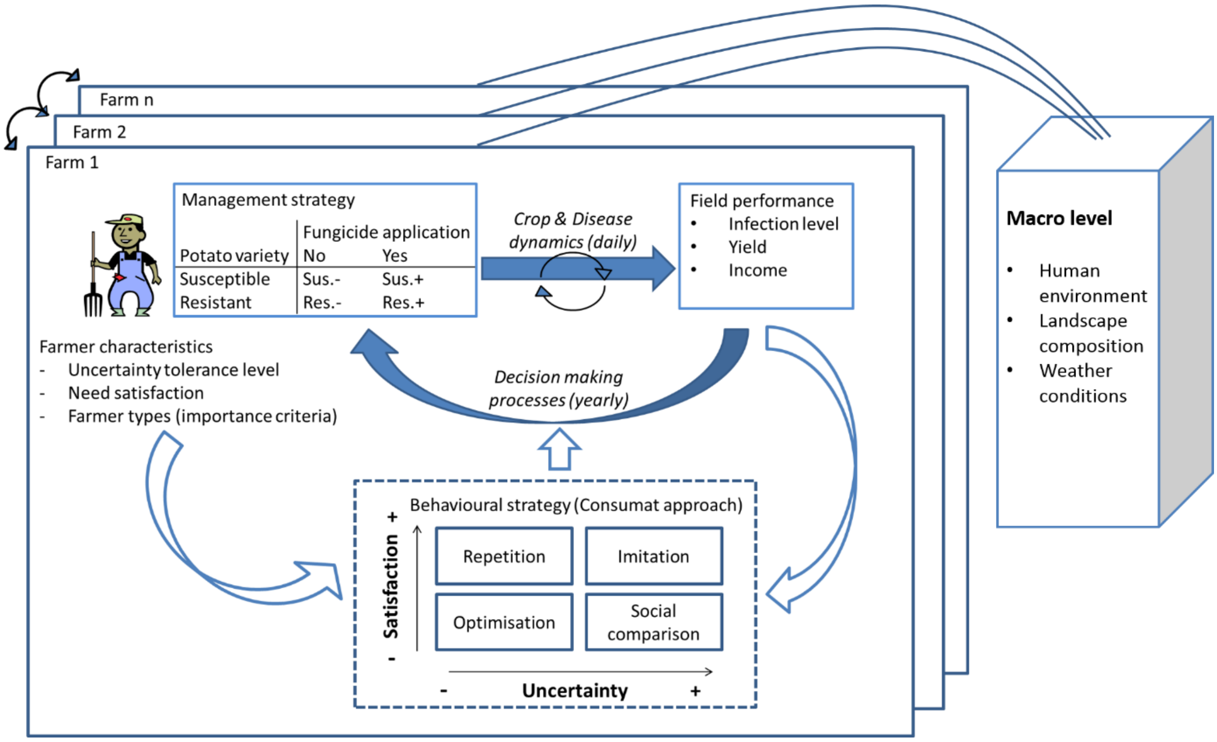

Figure 4.1. Conceptual overview of the model. Coloured arrows represent model processes and white arrows represent variables and frameworks used as input. Four management strategies are distinguished in the model: susceptible potato variety without fungicide application (sus-), susceptible variety with fungicide application (sus+), resistant variety without fungicide application (res-) and resistant variety with fungicide application (res+).

4.2.1 Model description

4.2.1.1 Model Overview

The model represents an agricultural landscape of 10 x 10 km^2. The potato density (24%) and the mean field size (±7 ha) were derived from landscape data of an agricultural region in the Netherlands (the Noordoostpolder) and these parameters were used as input for the model. The grid cells represent an area of 200 × 200 m^2 (4 ha), and are clustered in agricultural fields. Crop rotation was not taken into account. The model is populated by farmers each of whom manages one potato field. A network was initialised in which farmers are connected to the closest farmers around them (shortest spatial distance). Farmers use one of the following late blight management strategies: they can grow a susceptible or resistant late blight potato variety with or without the use of fungicides. These strategies have different effects on field and landscape performance. Field performance is analysed for criteria: infection level, yield and income. Landscape performance also relates to disease dispersal and resistance durability. A conceptual overview of the model is shown in Figure 4.1.

We simulate the growing season from May 1 to September 30 for 50 years. Crop growth and disease dynamics are updated at a daily time step. At the end of each growing season farmers analyse their field performance and select a management strategy for the following year. The decision-making framework to select a management strategy is based on the Consumat approach (Jager and Janssen, 2012; Janssen and Jager, 2001). Based on their field performance farmers determine their satisfaction and uncertainty level which results in one of the following behavioural strategies: repetition, imitation, optimisation or social-comparison (see Section 4.2.1.5). The decision-making process is influenced by personal characteristics including their need satisfaction and uncertainty tolerance level. Four farmer types are distinguished which differ in the weights assigned to the criteria (Table 4.1). The weights represent the importance of the different criteria to the farmer. Interaction between farms is related to social interaction with respect to farmers' decision making and spatial interactions related to disease dispersal.

Crop growth and late blight dynamics are simulated at grid cell level. We consider only one susceptible variety and one resistant potato variety (with a single resistance gene). Although the yield potential may increase in the coming years with the introduction of other resistant varieties, in our model we assume the resistant variety has a lower potential yield compared to the susceptible variety, which is reflected in the crop growth parameters. At the start of each growing season the infection is initialised in a fraction of the potato grid cells, randomly selected. When a grid cell is infected, spores are produced that are dispersed to nearby cells where they can cause infections. Two types of late blight are distinguished: the wild-type and the virulent strain. The wild-type can only infect the susceptible variety, while a virulent strain can also infect the resistant variety. At the start of the simulation only the wild-type is present. The virulent strain may emerge during the growing season as the result of mutations during spore production. The ratio between the wild type and virulent strain at the end of the growing season was used to calculate the number of initial infections of the wild type and virulent strain in the following year.

Since late blight development and crop growth are weather dependent, we used measured weather data from May 1 to September 30 (152 days) for 36 years (1981-2016) as model input. These years represent variable weather conditions for crop growth and late blight dynamics. To simulate crop growth, mean daily temperature and total radiation was calculated and used as input for the model. Secondly, based on calculation rules using hourly temperature and relative humidity during a 24-hour period, we determined whether a day was suitable for sporangia to cause infection (Skelsey et al., 2009a). Expansion of existing lesions occurs every time step but new infections as a result of spore germination can only occur on so-called 'blight days'. For more details we refer to Chapter 3. At the start of each year a dataset is randomly selected out of these 36 years of weather data.

Table 4.1. Overview of farmer types in the model which differ in the weights assigned to the criteria on infection level, potato yield and income. The weights represent the importance of the different criteria to the farmer. Farmers need satisfaction and uncertainty tolerance level are randomly selected between 0 and 1.

Farmer type	Description	Need satisfaction	Uncertainty tolerance level	Weight of yield criterion (w_p)	Weight of income criterion (w_y)	Weight of infection level criterion (w_d)
1	Yield maximizer	0-1	0-1	0.8	0.1	0.1
2	Profit maximizer	0-1	0-1	0.1	0.8	0.1
3	Risk aversive farmer	0-1	0-1	0.1	0.1	0.8
4	Neutral farmer	0-1	0-1	0.33	0.33	0.33

4.2.1.2 Late blight management strategies in the model

In the Netherlands the use of fungicides is currently the most widely used method in the control of late blight while crop resistance has been identified as an important strategy for more sustainable control (Haverkort et al., 2008; Lammerts van Bueren et al., 2008). Combining these two types of disease control results in the following four strategies: growing a susceptible potato variety with (sus+) or without fungicide application (sus-), or growing a resistant potato variety with (res+) or without fungicide application (res-). In the model farmers select one of these strategies for their potato field (Figure 4.1). The management strategies can be related to current farm practices of conventional and organic farmers. In conventional agriculture, mainly susceptible varieties are grown combined with fungicide application (sus+). Since chemical control is not allowed in organic potato production and not enough resistant potatoes are available to supply the whole market (Bionext, 2017), organic farmers grow a combination of susceptible and resistant varieties and do not apply fungicides (sus- and res-). In years with early outbreaks of the disease, organic farmers can therefore suffer high yield losses in susceptible fields, but in years with a low infection pressure farmers can make a profit. Combining a resistant variety with (reduced use of) fungicides (res+) has been proposed to prevent resistance breakdown and to increase resistance durability (Haverkort et al., 2016). Although we do not distinguish organic and conventional potato production in the model, the late blight management strategies represent the different approaches in late blight control.

In case fungicides are used on susceptible and resistant fields (sus+ and res+), weekly application is assumed starting at the day of crop emergence. Weekly application is standard practice for many potato farmers, also because it is combined with the application of other chemicals for other diseases. Decision support systems (DSS) are available that can help farmers to improve efficiency of spraying by optimizing the use and timing of fungicide application. However, many farmers do not strictly follow their advice. Over the season farmers use different type of chemicals. In the model we distinguish preventive and curative fungicides. We assume preventive fungicides are applied at the start of the growing season to reduce the infection efficiency of the spores. When the disease severity in potato grid cells reaches 1%, curative fungicides are applied which have a similar effect on the infection efficiency, but also reduce the expansion of existing lesions.

To prevent spread of the disease during the growing season the government has implemented a policy that regulates maximum late blight disease thresholds (NVWA, 2008). At an estimated disease severity of 5% in the field, the potato haulm has to be destroyed. An inspection system was set up, including an anonymous hotline, that could fine farmers in case these regulations were not followed. Following these regulations we assume that all farmers in the model destroy the potato haulm when the disease severity in potato grid cells reaches 5%. This means that leaf and tuber growth stops directly and the disease can no longer disperse to other fields. In case of early outbreaks of the disease, this can cause severe yield losses.

4.2.1.3 Analysing field performance

In the model we implemented three criteria to evaluate the field performance of farmers: late blight infection level, potato yield and income. Infection level is an important criterion to evaluate the effectiveness of the selected management strategy and infection in a field can also reduce potato yield and farmer income. Furthermore, late blight management strategies include trade-offs between infection level, yield and income. The application of fungicides can reduce the risk of infection and prevent yield losses but causes additional costs. Growing a resistant variety can reduce the risk of infection, but has a negative effect on potato yield and income since we assume that the resistant variety has a lower potential yield compared to the susceptible variety. In addition, growing a resistant variety creates a risk on resistance breakdown by emergence of a new virulent strain. To evaluate the field performance in relation to late blight management strategies it is therefore important to consider all three criteria. Secondly, the importance of these criteria also differs between farmers (Table 4.1).

Infection level

In the model, late blight severity (percentage of infected leaf tissue) within a field is affected by the weather conditions, disease dispersal and late blight management strategies (fungicide use and crop resistance). The simulated disease severity ranged from no or very low disease severity to a very high disease severity (10^{-4} % to >5%). Development of the disease at field level is limited since we assume that the potato haulm is destroyed when disease severity reaches 5%. In practice in the field disease severity is generally estimated visually. Because the human eye can estimate low and high disease severity more precisely than mid-range levels, it is proposed to correct this by using a logarithmic rather than a linear scale (Cooke, 2006). Taken these factors into account a scale from 1 to 4 was developed to analyse the infection level using data on disease severity: 1: < 0.1%, 2: 0.1 -1%, 3: 1-5%, 4: >5%.

Potato yield

At the end of the growing season the mean potato yield (tonnes/ha) of farmers is calculated. Potato yield is affected by the potato variety, weather conditions including temperature and radiation, and infection with late blight. In the model we assume that the resistant potato variety has a 20% lower potential yield compared to the susceptible variety.

Income

We use a standard approach to calculate farmer income: farmers' gross margin (€ ha^{-1}) is based on the actual potato yield times the price for potatoes minus production costs. With respect to production costs we only consider the costs related to fungicide application since we focus on comparing late blight management strategies. Costs for fungicides are related to the number of applications, the type of fungicides used, machinery, labour and fuel. The mean number of applications per farmer was calculated over the year (assuming weekly application) and the costs per application (f_c) were estimated at €50 ha^{-1} (Haverkort et al., 2008). The price for potatoes was set on €13 per 100 kg which was derived from a dataset on potato prices for conventional ware potatoes in the Netherlands between 2000 and 2017 (WUR, 2018). The same price was used for the susceptible and resistant variety. Correlations between potato price and overall potato yield were not included in the model since in reality these factors are also affected by many other processes not included in the model. For example the crop price is mainly dependent on the market farmers produce for (e.g. organic, conventional, frozen and fry, table and fresh) (Haverkort et al., 2008; Pavlista and Feuz, 2005).

4.2.1.4 Farmer population

Many studies have shown the importance of social interactions within networks in decision making processes, also with respect to Dutch farmers (Oerlemans and Assouline, 2004; Van Duinen et al., 2016). According to the Consumat approach agents are influenced through interactions within networks when they engage in social comparison or imitation. Unfortunately no empirical data was available on social networks among Dutch potato farmers, however, previous results from interviews showed that potato farmers influence each other and copy each other's behaviour (Chapter 2). Since farmers have social interactions (e.g. as neighbours, friends and in study groups) and they spend much time on their land they are well aware how surrounding farmers manage their crops. Potato late blight disperses by wind so infections in neighbouring fields can increase the risk of infection. With respect to social interaction on late blight control we therefore assume farmers are in a network with the closest farmers around them (shortest distance between fields). In each model run, a network is initialised in which farmers are connected to the closest farmers around them (with a mean number of 5 links per farmer), representing a social network of neighbours. We explored the effect of alternative network structures. Increasing the mean number of links per farmer from 5 to 10 links did not affect the model results as well as a different network setup in which farmers are connected to the closest farmers around them of the same type, assuming that you interact more with people who are more similar to you.

To create a heterogeneous population, characteristics of farmers are varied within a certain range. Farmers uncertainty tolerance level and need satisfaction are randomly selected between 0 and 1. We distinguish four farmer types which differ in the weights assigned to the criteria used to analyse field performance: infection level, yield and income (Table 4.1). The weights represent the importance of the criteria to the farmer in their decision making. Based on these preferences farmers have different objectives resulting in four farmer types: yield maximizer, profit maximizer, risk aversive farmer and neutral farmer. At the start of the simulation the farmer type of each farmer is randomly selected. Profit and yield maximizing farmers are types previously described in the literature (Malawska and Topping, 2016). Furthermore, studies have shown that farmers can have different risk attitudes which influences decision making on disease control (McRoberts et al., 2011; Willock et al., 1999). Risk perception in late blight control can for example be related to the size of potential negative impact of infection on yield and income (Chapter 2). In the model the risk-aversive farmers therefore aim to minimize the infection level in their field.

4.2.1.5 Behavioural strategies

According to the Consumat approach, behaviour of agents is affected by the levels of satisfaction and uncertainty. To determine farmers' satisfaction and uncertainty the actual (a_i), potential (p_i) and predicted (e_i) performance is calculated for the three criteria: infection level, yield and income. The potential field performance is the maximum result which could be achieved in a specific year without any losses as a result of yield-limiting and yield-reducing factors (Van Ittersum and Rabbinge, 1997). In our model we only consider losses as a result of infection with the disease. The potential yield of both potato varieties is based on the temperature and radiation in a specific year. The potential income is calculated in the same way as the actual income but using the potential yield. The potential infection level was set at 1 which represents the lowest level of disease severity that could be achieved.

Farmers also estimate the field performance for the coming year. For each performance criterion they calculate the mean value using historical values of their own field for the last five years. To create a list of reference values the model is run for five years before the actual simulation starts (see Appendix 4.A). In the model, satisfaction is defined as the ratio between the actual and the potential performance, and uncertainty as the ratio between the actual and the estimated (predicted) performance. For each performance criterion the satisfaction and uncertainty is calculated. The overall satisfaction (S_t) and uncertainty (U_t) is based on the result for each criterion (i) influenced by the weights (w_i) (Equations 4.1 and 4.2).

$$S_t = \sum w_i a_i / p_i \qquad (4.1)$$

$$U_t = \sum w_i a_i / e_i \qquad (4.2)$$

Farmers compare their total satisfaction and uncertainty level with their personal need satisfaction and uncertainly tolerance level. If the results are below their thresholds, farmers are uncertain and/or unsatisfied. Based on these results farmers engage in one of the following behavioural strategies. If a farmer is satisfied and certain he will repeat its current behaviour and continue using the same management strategy. If a farmer is uncertain he will interact with other farmers in his network to make an informed decision. Agents who are uncertain are more likely to engage in strategies that involve interactions, while agents who are certain are more likely to rely on their own experiences. If a farmer is uncertain but satisfied he will engage in imitation. In this case he will adopt the management strategy that is used by the majority of farmers in his network. When farmers are unsatisfied they engage in strategic decision making. This strategy relates to rational decision making in which farmers are aiming to optimize their field performance in relation to their preferences. First they select the criterion which they want to optimize: infection level, yield or income. This is based on the satisfaction level for each criterion, and on the criteria weights. In case farmers are unsatisfied and uncertain, they engage in social comparison. In this strategy farmers analyse the field performance of the farmers in their network and adopt the management strategy of the farmer that has the highest score for the specific criteria. When farmers are unsatisfied but certain, they engage in optimising behaviour. In this case they compare the mean field performance of all management strategies of the last year and adopt the management strategy that has the highest result for the criteria they want to improve. When the resistant variety with and without fungicides have the same score for a criterion it is assumed that farmers select the resistant variety without fungicides.

4.2.2 Scenario analysis

We assumed a situation where a new resistant variety was introduced to the market. We analysed the effect on disease control by adoption of the resistant variety by farmers and the durability of resistance. At the start of the simulation all farmers are growing a susceptible variety and the majority applies fungicides (90%). Three scenarios were explored in which we analysed the effect of higher fungicide costs and higher yield or potato price of the resistant variety. These changes represent possible future scenarios as a result of actions by stakeholders.

First we increased the yield potential of the resistant potato variety so it is similar to the susceptible variety (yield-scenario). Breeding companies continue to develop new late blight resistant potato varieties and it is likely that in the future new resistant varieties will be introduced with higher yield levels. Secondly, as a result of stakeholder cooperation, the price for resistant varieties could increase in the future. In the standard settings the crop price of resistant and susceptible varieties was the same. Recently, the organic sector made an agreement to upscale the production of resistant varieties to completely service the organic market over the coming years (Bionext, 2017). An increase in demand could also result in a higher crop price. In the price-scenario we therefore increased the price of the resistant variety by 25%.

In the third scenario (fungicide-scenario) we doubled the price per fungicide application (from € 50 ha^{-1} to € 100 ha^{-1}). About half of all fungicides applied in the Netherlands are used in the control of late blight. The environmental costs are related to the pollution of groundwater, energy costs for application and negative effects on human health (Haverkort et al., 2008). Increased environmental awareness could possibly lead to higher prices for fungicides, for example, when government increases taxes. We analysed how these changes could affect the adoption of management strategies by farmers and the control of late blight.

To analyse the model results a number of output variables were calculated at the end of each growing season. We recorded the behavioural strategies and management strategies of farmers as well as the mean performance per strategy for the criteria infection level, yield and income. To analyse disease dynamics we calculated the disease incidence (the percentage of infected potato grid cells with a disease severity ≥ 1%) (Skelsey et al., 2010) and the infected resistant fields (the percentage of resistant potato grid cells in the landscape infected with the virulent strain). We also recorded the year infections in resistant fields were observed followed by establishment of the virulent strain in the population (year of resistance breakdown). This occurs as a result of between year survival of the virulent strain resulting in initial infections in the following year. For each scenario, simulation runs were repeated 100 times.

4.3 Results

4.3.1 Dynamics over time

4.3.1.1 Example of two model runs

After 50 years of simulation we observed two different patterns. In the first pattern at some moment during the simulation infections in resistant fields were observed and the virulent strain established in the population (Figures 4.2a-4.2f), while in the second pattern this process was not observed (Figures 4.2g-4.2l). So in the first pattern resistance breakdown occurred while in the other pattern resistance remained effective during the simulation time. To analyse the dynamics over time an example of one model run of both patterns is shown in Figure 4.2.

From the start of the simulation in both patterns the number of susceptible fields decreased and the number of resistant fields increased (Figures 4.2a and 4.2g). Susceptible fields without fungicide application had a high risk of infection, and yield and income are fluctuating strongly as a result of the weather conditions that affect spread of the disease. Fungicide application on susceptible fields could not prevent infection completely but no large losses in yield and income were observed. Due to infection with late blight farmers were unsatisfied with their field performance which led to optimizing behaviour (Figures 4.2f and 4.2l). Farmers that optimized on infection level adopted the resistant variety since this strategy scored better on infection level as a result of crop resistance (Figure 4.2b and 4.2h). In the model it was assumed that farmers won't apply additional fungicides on the resistant variety when the resistance is effective so farmers adopted the resistant variety without fungicides.

In both simulation runs after a couple of years a small percentage of resistant fields was infected by emergence of a virulent strain (Figures 4.2e and 4.2k). However, in pattern 2 the virulent strain was not able to spread and establish in the population. A small number of farmers responded to this event and switched to the resistant variety with fungicide application (Figure 4.2g).

In pattern 1 after 8 years the virulent strain was able to establish in the population and the percentage of infected resistant fields rapidly increased over time (Figures 4.2e and 4.3). As a result of the relative high percentage of resistant fields (±20%) the virulent strain could spread fast through the landscape which gave farmers a very short time to adapt. When the percentage of infected resistant fields reached 55% the percentage of farmers growing a resistant variety without fungicides started to decrease. The spread of the virulent strain led to simulated losses in yield and income of resistant fields, which resulted in reduced farmer satisfaction and increased uncertainty, and farmers switching to other management strategies.

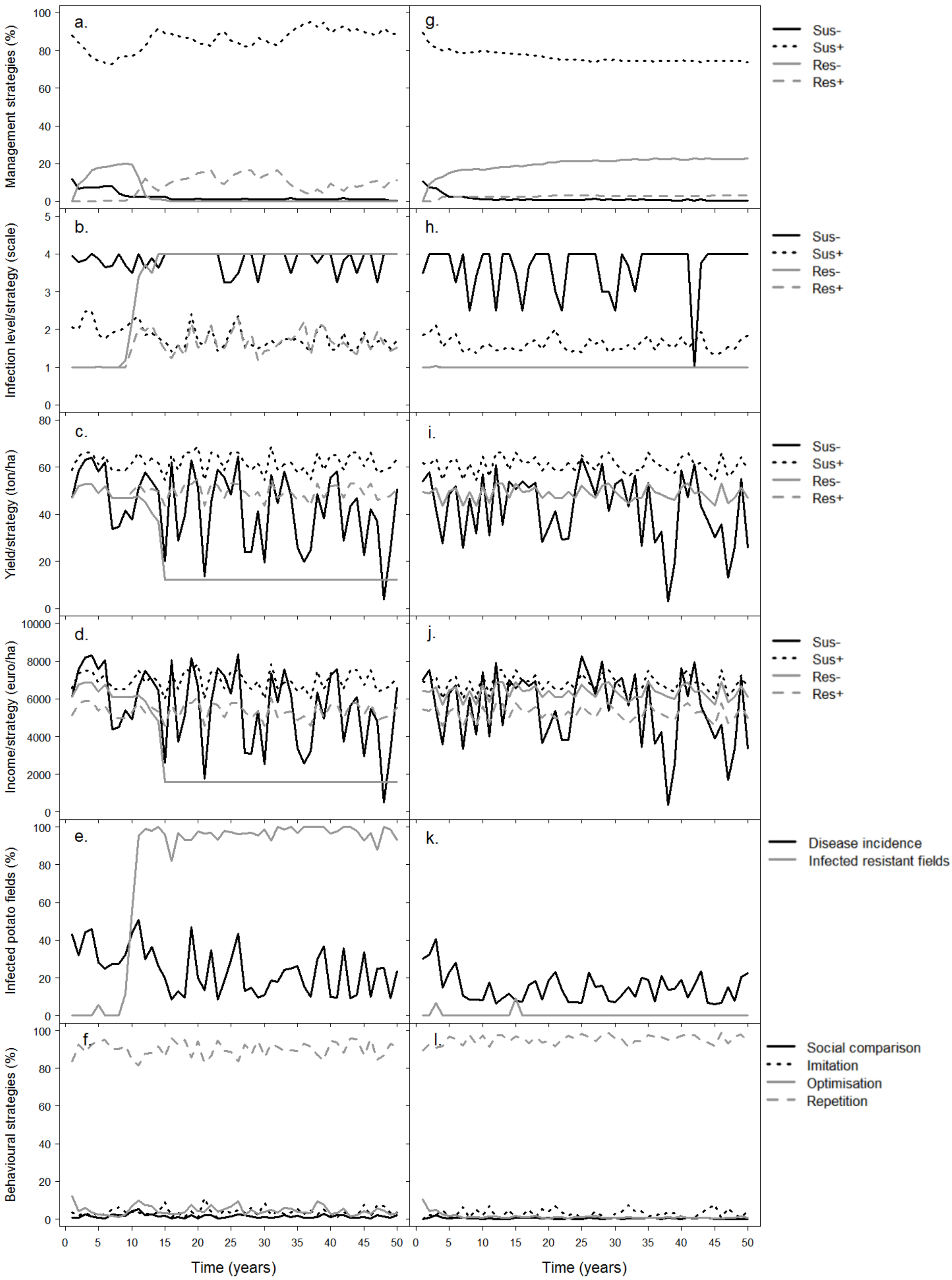

Figure 4.2. Example of two model runs with (a-f) or without (g-l) crop disease-resistance breakdown. In the figures we show the management strategies of farmers (a and g), the mean field performance per management strategy for the criteria infection level (b and h), yield (c and i) and income (d and j), the spread of the disease in the landscape using the disease incidence and the infected resistant fields (e and k) and the behavioural strategies of farmers (f and l).

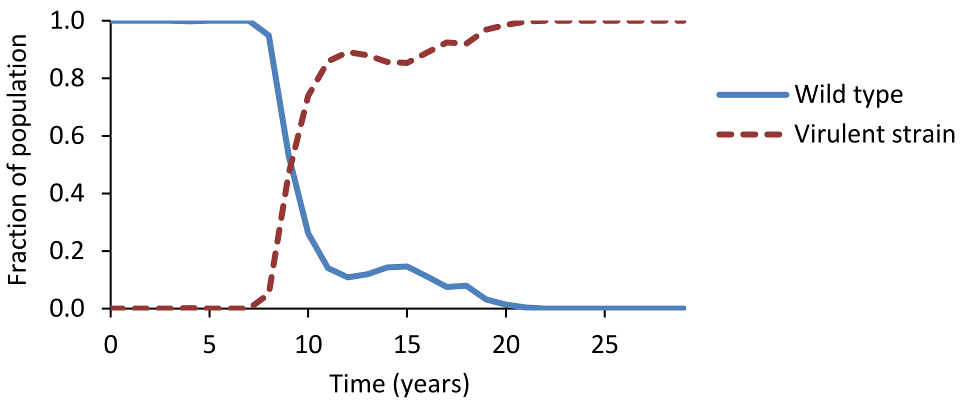

Figure 4.3. Population dynamics of late blight showing the emergence and spread of the virulent strain. The figure presents an example of one model run in which resistance breakdown occurred (see also Figure 4.2) and shows the proportion of disease severity caused by infection with the wild-type (solid line) and virulent strain (dashed line).

Social comparison and imitation mainly led to the adoption of the susceptible variety with fungicide application since this management strategy is used by the majority of the farmers and resulted in a lower infection level and higher yield and income. Optimising behaviour on infection level led to the adoption of the resistant variety with fungicide application. However, because the virulent strain was already present in the population, additional fungicide application only slowed down infection within the field, but could not eradicate the virulent strain from the landscape. As a result, the infection level in fields with the initially resistant variety increased, and yield and income of resistant fields without fungicides decreased. Since the resistant variety had a lower potential yield compared to the susceptible variety at some point the yield of resistant fields without fungicides dropped below the yield of susceptible fields without fungicide application. Within five years after the first resistant fields were infected almost no farmers were growing the resistant variety without fungicides anymore. The majority of farmers adopted the susceptible variety with fungicides and a small number of farmers the resistant variety with fungicides (Figure 4.2a). The resistant variety with fungicides had a lower level for yield and income but in some years had a lower infection level. After resistance breakdown the disease incidence in the landscape was highly variable per year. A small fraction of farmers remained unsatisfied and/or uncertain resulting in social comparing, optimising and imitating behaviour. However, no alternative strategies were available that led to a significant improvement.

In the simulation runs in the baseline scenario where resistance was still effective after 50 years, the percentage of farmers growing a resistant variety stabilized at 19.5% ±3.1 (SD) (Table 4.2). This was also observed in the example shown in Figure 4.2b. The majority of farmers was growing the susceptible variety with fungicide application (79.0% ±2.4). Most farmers were satisfied and certain about their field performance and engaged in repeating behaviour which resulted in a stable situation with respect to late blight management strategies.

Table 4.2. Management strategies of farmers (%) at the end of the simulation (year 50) in case resistance breakdown occurs and in case the resistance remains effective. Mean values are shown (±SD) based on 100 runs.

	Management strategies of farmers (%)			
	Sus-	Sus+	Res-	Res+
Resistance breakdown occurs				
Baseline	0.9 ±0.7	92.0 ±3.7	0.2 ±1.4	6.9 ±3.5
Higher fungicide costs	1.1 ±1.2	92.1 ±4.2	0.3 ±2.5	6.4 ±3.7
Higher crop price resistant variety	0.8 ±0.5	90.2 ±4.7	0.8 ±4.3	8.2 ±3.8
Higher yield resistant variety	0.9 ±0.5	88.1 ±4.8	0.1 ±0.6	10.9 ±4.7
Resistance remains effective				
Baseline	0.6 ±0.6	79.0 ±2.4	19.5 ±3.1	1.0 ±1.9
Higher fungicide costs	0.5 ±0.5	74.2 ±3.2	25.0 ±3.2	0.2 ±0.6
Higher crop price resistant variety	0.5 ±0.4	74.8 ±3.3	24.5 ±3.4	0.3 ±0.9
Higher yield resistant variety	0.4 ±0.4	72.0 ±3.0	27.0 ±2.9	0.6 ±1.4

Table 4.3. Year of resistance breakdown as a result of establishment of the virulent strain in different scenarios. For each scenario the model was run 100 times.

Year resistance breakdown (percentage of runs)	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**	**>50**
Baseline	41	17	5	4	6	27
Higher fungicide costs	44	18	5	5	1	27
Higher crop price resistant variety	46	9	7	2	5	31
Higher yield resistant variety	44	11	4	5	1	35

4.3.1.2 Time until resistance breakdown

The year of emergence of infections in resistant fields followed by establishment of the virulent strain in the population was analysed (Table 4.3). Resistance breakdown was observed in 73% of the model runs. In 42% of the model runs establishment of the virulent strain occurred in the first 10 years after the introduction of the resistant variety followed by an additional 17% during the ten following years. Once this period had passed the risk of establishment decreased. In 27% of the model runs the resistance was still effective after 50 years. The first years after introduction of the resistant variety a larger number of farmers was growing a susceptible variety without fungicide application. These fields could act as sources of infection and there was an increased risk that the virulent strain emerged. In the year the virulent strain established in the population the mean percentage of farmers that used a susceptible variety without fungicides was 2.0% ±1.5. After this first period the risk of establishment decreased as a result of a lower fraction of susceptible fields without fungicides. However, as long as farmers are present that grow the susceptible fields without fungicides resistance breakdown can occur, which was also observed in the model after 30 or 40 years.

4.3.1.3 Farmer characteristics

We analysed the personal characteristics of farmers per management strategy at the end of the simulation (Table 4.4). Farmers growing a susceptible variety without fungicides mainly had a low need satisfaction (0.35) and uncertainty tolerance level (0.31). As a result they mainly engaged in repeating behaviour and the farmers growing the susceptible variety without fungicides from the start of the simulation were less likely to change their strategy. Since this strategy resulted in most years in a higher infection level, lower yield level and lower income compared to the other strategies (Table 4.5), almost no farmers adopted this strategy during the simulation.

Farmers growing a resistant variety with or without fungicides had a relative high need satisfaction (0.72-0.75) and also a high value for the weight infection level (0.62), which shows that these were mainly risk-aversive farmers (Table 4.1). Unsatisfied farmers engaging in optimizing behaviour related to infection level would select the resistant variety without fungicide application and after infections in resistant fields, the resistant variety with fungicides. However, when both of these strategies were not effective anymore to prevent infection they switched to other strategies.

Farmers growing the susceptible variety with fungicides were a large group of farmers. The weights for the criteria infection level, yield and income were almost equal and standard deviations were high, which indicates that these farmers were a mix of yield optimizers, income maximizers and neutral farmers. In the baseline scenario the susceptible variety with fungicide application resulted in the highest yield and income (Table 4.5). Growing the susceptible variety with fungicides did not result in losses in yield and income as a result of infection and therefore many farmers continued using this strategy.

Table 4.4. Characteristics of farmers per management strategy at the end of the simulation (year 50). Mean values are shown (±SD) based on 100 model runs. At the start of the simulation farmers' uncertainty tolerance level and need satisfaction were randomly selected between 0 and 1. The weights represent the importance of the criteria to the farmer in their decision making. The weights are dependent on the farmer type shown in Table 4.1.

Management strategy	Need satisfaction	Uncertainty tolerance level	Weight infection level	Weight yield	Weight income
Sus-	0.35 ± 0.40	0.31 ± 0.24	0.41 ± 0.32	0.21 ± 0.21	0.38 ± 0.31
Sus+	0.48 ± 0.28	0.51 ± 0.29	0.30 ± 0.27	0.35 ± 0.30	0.35 ± 0.29
Res-	0.72 ± 0.22	0.50 ± 0.28	0.61 ± 0.24	0.19 ± 0.13	0.19 ± 0.15
Res+	0.75 ± 0.19	0.40 ± 0.26	0.62 ± 0.23	0.19 ± 0.12	0.19 ± 0.12

Table 4.5. Mean performance per management strategy for the criteria infection level, yield and income per scenario: B= Baseline, F=Higher fungicide costs, P=Higher potato price resistant variety, Y=Higher yield resistant variety. Mean values (±SD) are shown based on 100 runs. Model results in the baseline scenario are highlighted in grey.

	Scenario	Sus-	Sus+	Res-	Res+
Resistance breakdown occurs					
Infection level (-)	B	3.8 ± 0.4	1.8 ± 0.3	3.4 ± 0.9	1.7 ± 0.4
	F	3.9 ± 0.4	1.8 ± 0.3	3.6 ± 0.8	1.8 ± 0.4
	P	3.9 ± 0.3	1.8 ± 0.3	3.6 ± 0.7	1.7 ± 0.4
	Y	3.9 ± 0.4	1.8 ± 0.3	3.7 ± 0.7	1.7 ± 0.5
Yield (t ha^{-1})	B	42.2 ± 15.3	61.9 ± 3.5	37.7 ± 11.9	49.5 ± 2.8
	F	41.9 ± 15.5	61.9 ± 3.6	36.4 ± 13.1	49.6 ± 2.9
	P	42.2 ± 15.4	62.0 ± 3.5	35.4 ± 13.0	49.5 ± 2.9
	Y	42.5 ± 15.4	61.9 ± 3.5	44.3 ± 15.8	61.9 ± 3.3
Income (€ ha-1)	B	5488 ± 1995	6950 ± 454	4900 ± 1546	5335 ± 362
	F	5445 ± 2017	5863 ± 469	4734 ± 1700	4265 ± 382
	P	5482 ± 2003	6963 ± 460	5761 ± 2110	6954 ± 470
	Y	5524 ± 1996	6958 ± 460	5765 ± 2060	6949 ± 430
Resistance remains effective					
Infection level (-)	B	3.8 ± 0.5	1.8 ± 0.3	1.0 ± 0.1	1.0 ± 0.0
	F	3.7 ± 0.5	1.7 ± 0.3	1.0 ± 0.1	1.0 ± 0.0
	P	3.7 ± 0.6	1.7 ± 0.3	1.0 ± 0.0	1.0 ± 0.0
	Y	3.7 ± 0.6	1.7 ± 0.3	1.0 ± 0.0	1.0 ± 0.0
Yield (t ha^{-1})	B	43.3 ± 14.9	61.9 ± 3.5	49.6 ± 2.8	49.6 ± 2.8
	F	43.8 ± 14.6	61.9 ± 3.6	49.6 ± 2.9	49.6 ± 2.8
	P	44.5 ± 15.0	62.1 ± 3.5	49.7 ± 2.8	49.7 ± 2.7
	Y	44.4 ± 15.0	61.9 ± 3.5	61.9 ± 3.6	62.1 ± 3.5
Income (€ ha-1)	B	5623 ± 1934	6960 ± 454	6452 ± 363	5344 ± 365
	F	5697 ± 1898	5862 ± 473	6446 ± 377	4249 ± 369
	P	5790 ± 1952	6980 ± 458	8071 ± 460	6980 ± 446
	Y	5775 ± 1957	6958 ± 457	8051 ± 461	6978 ± 461

4.3.2 Scenario analysis

To compare the model scenarios, we analysed the management strategies of farmers after 50 years of simulation for the two patterns: with and without resistance breakdown (Table 4.2). Also the year resistance breakdown occurred was analysed as well as the mean field performance per management strategy (Tables 4.3 and 4.5). Overall we observed small effects of higher parameter values related to costs for fungicide application, yield level of the resistant variety and crop price of the resistant variety with respect to management strategies of farmers. In the situation where resistance breakdown occurred the percentage of farmers growing a resistant variety without fungicides remained low in all scenarios but the percentage of farmers growing a resistant variety with fungicides slightly increased in case of a higher crop price and higher yield level of the resistant variety (Table 4.2). When resistance was overcome by the pathogen the mean field performance of the resistant variety was lower or equal compared to the susceptible variety with fungicides in all scenarios (Table 4.5).

When resistance remained effective the percentage of farmers growing a resistant variety without fungicides increased from 19.5% to maximum 27.0%. Increasing the yield level of the resistant variety had the largest effect since this resulted in a higher yield and income. In all three scenarios the resistant variety without fungicides resulted in a higher income compared to the susceptible variety with fungicides (Table 4.5). However, many farmers who started with the susceptible variety with fungicide application continued using this strategy because fungicides effectively suppress the disease so stable levels in yield and income are achieved. As a result, farmers were satisfied and certain and mainly engaged in repeating behaviour.

Differences in management strategies as a result of higher parameter values related to costs for fungicide application, yield level of the resistant variety and crop price of the resistant variety did not have a strong effect on resistance breakdown (Table 4.3). Some variation was observed mainly during the first 20 years of the simulation but this was probably the result of random processes such as the weather conditions and the allocation of potato fields since no large differences between management strategies were observed.

4.4 Discussion

Boom-and-bust cycles

Simulating the interactions between farmers' decision making and late blight dynamics increased understanding on the effects of adoption of a resistant potato variety by farmers on disease dynamics and resistance durability. Assuming a scenario where a new resistant variety with a single resistance gene became available, the model showed a gradual increase of farmers growing the resistant variety. In the majority of model runs resistance breakdown occurred within the first 20 years of the simulation by emergence of a new virulent strain. The virulent strain spread over the landscape and became dominant in the late blight population, decreasing yield and income of resistant fields. In the model, farmers responded to this event by switching to other management strategies, mainly to growing the susceptible variety with fungicide application.

This pattern has been described previously as a boom-and-bust cycle because of the often rapid rise and fall in the effectiveness of host resistance against pathogen populations in agriculture (Brown and Tellier, 2011; Pink and Puddephat, 1999). One cycle includes several stages: a) introduction of a resistant variety with a novel resistance gene source, b) increase in use of the resistant variety, c) emergence of a new virulent strain, d) a rapid increase of the virulent strain in the population, e) the complete loss of resistance in the crop, f) decrease in use of the variety with the specific resistance gene followed by g) decline of the virulent strain in the population (assuming fitness costs are associated to virulence). The cycle can be repeated multiple times when varieties are introduced with new resistance traits.

For potato late blight, boom-and-bust cycles have been observed after the introduction of resistant varieties from earlier breeding programs (Fry 2008). When varieties were introduced containing resistance genes from the closely related species *Solanum demissum* new virulent strains emerged that overcame resistance (Malcolmson, 1969). Boom-and-bust cycles are a general phenomenon in monocultures with gene-for-gene interactions and have also been described in other crops including oilseed rape, wheat and barley (De Vallavieille-Pope et al., 2012; Rouxel et al., 2003; Wolfe and McDermott, 1994).

In our model we assumed that no costs are associated with virulence hence the virulent strain did not decline in the population when farmers stopped growing the variety with the matching resistance gene. According to experimental data no or only few relations between fitness costs and virulence have been found (Montarry et al., 2010; Schöber and Turkensteen, 1992). In other crops it has been observed that virulent strains rarely revert to their initial frequencies after removal of the variety with the corresponding resistance gene (Mundt, 2014). This is relevant information with respect to deployment strategies such as gene rotation or stacked resistance with previously defeated resistance genes. If virulent strains remain present in the pathogen population these resistance management strategies will be less effective because the virulent strains can rapidly reproduce after reintroduction of resistance genes, or more easily adapt to varieties with multiple resistance genes when one of these genes has already been overcome.

A number of theoretical models exist that reproduced boom-and-bust cycles by simulating host-pathogen interactions at the landscape scale (Brown and Tellier, 2011), but as far as we know none of these included the interactions with respect to farmers' decision-making. By exploring the interactions between farmer behaviour and the spatially explicit evolutionary dynamics of the pathogen we identified potential factors and processes that could affect the adoption of a resistant potato variety and resistance durability. These factors and the implications for disease management are described in the following sections.

Scenario analysis

The results from this study showed that in the current situation the use of susceptible varieties with fungicide application resulted in the highest yield and income which is in line with current management strategies of conventional farmers. In all model scenarios almost no farmers were growing the susceptible variety without fungicides since this strategy resulted in most years in a high infection level and losses in yield and income. The organic sector currently represents about 1% of the total potato production area in the Netherlands. Due to severe late blight outbreaks between 2000 and 2007 and a lack of resistant varieties its acreage decreased by 20%, showing that growing susceptible varieties without any effective control is not profitable in years with high disease pressure, even with a premium price for organic potatoes (Lammerts van Bueren et al., 2008).

The scenarios including higher fungicide costs and higher yield or potato price of the resistant variety affected the field performance of management strategies, and consequently the selection of management strategies by farmers (Tables 4.2 and 4.5). When the resistance remained effective all three scenarios resulted in a higher yield and income of resistant fields without fungicides compared to susceptible fields with fungicides. As a result, more farmers adopted the resistant variety in the model and therefore these strategies could contribute to sustainable disease control. However, the risk on resistance breakdown was high and when the resistance was overcome farmers switched back to the use of fungicides. Farmers in the model were simulated as social agents who interacted with each other and the environment. Simulating the social-ecological interactions can increase insight in the potential effects of certain policies or changes in the socio-economic environment and be used to identify strategies that foster a transition towards more sustainable disease management.

Regime shifts

The model showed that resistance breakdown did not occur in all simulation runs. Emergence of virulent spores as a result of mutation has a low probability. In addition, spread of the virulent strain is affected by processes such as the weather conditions and allocation of potato varieties which varies between years and model runs. Resistance breakdown as a result of emergence and spread of the virulent strain in the late blight population could be described as a regime shift (Filatova et al., 2016). A regime shift transforms the system resulting in new properties, structure, feedbacks, and underlying behaviour of components or agents. When resistance breakdown occurred in the model the system changed with respect to the field performance of management strategies, farmer behaviour and the pathogen population (Figures 4.2 and 4.3). Regime shifts can occur as a result of gradual changes in the system components or from interactions between processes operating at different spatial and temporal scales. In the model establishment of the virulent strain occurred when the ratio between the wild type and virulent strain exceeded a threshold resulting in initial infections of the virulent strain in the following year. This threshold can be reached when the virulent strain is able to emerge and spread during the growing season which is affected by the management strategies of farmers as well as a number of random processes such as the weather conditions, the allocation of farmers and potato fields and the location of infection sources at the start of the growing season.

Predicting critical transitions is often very difficult because the state of the system may show little change before the tipping point is reached (Scheffer et al., 2009). With respect to late blight control it has been suggested to set up monitoring programmes to yield direct insight in the *P. infestans* adaptation process at population level (Haverkort et al., 2016; Kessel et al., 2018). When a virulent strain is detected and the resistance is at risk of being overcome, additional management strategies are needed, for example by additional application of fungicides on resistant fields. In the model farmers growing a resistant variety started applying additional fungicides but after infections in resistant fields were observed. At this point the application of fungicides could only slow down spread of the virulent strain but the resistance was already overcome. Monitoring programmes could therefore be very useful to inform farmers about the risk on infections in resistant fields so additional measures are taken before the virulent strain will spread in the population.

Implications for late blight control

The model showed that the risk on emergence of new virulent strains and resulting infections in resistant fields was mainly high during the first 10 years after the introduction of resistant variety. During this period the number of farmers growing the resistant variety gradually increased and farmers growing the susceptible variety without fungicides decreased. In this transition period there is a higher risk that virulent spores emerge from susceptible fields and spread to neighbouring resistant fields. This is relevant information since stakeholders in the Dutch organic potato sector recently agreed to upscale the use of late blight resistant varieties (Bionext, 2017). There is currently insufficient supply of resistant seed potatoes for the entire organic market so the coming years a situation will occur were organic farmers will grow partly susceptible and partly resistant varieties. During this transition phase organic farmers must be aware of the risk of resistance breakdown and take immediate countermeasures when they observe infections in resistant fields. The model showed that in some years a small fraction of resistant fields was infected but the virulent strain was not able to establish in the population. Therefore a strategy that could be used by farmers to increase resistance durability includes immediate haulm destruction to prevent spread and establishment of the virulent strain in the late blight population.

The results showed that when resistance remained effective only part of the farmer agents in the model adopted the resistant variety, even when this resulted in a higher yield and income compared to the susceptible variety. We started with a situation in which the majority of farmers was growing the susceptible variety with fungicides. The model showed that the effect of habitual behaviour is very strong which means that when farmer agents are satisfied and certain, they would not change their management strategy. Although fungicides could not prevent infection completely, they suppressed the disease so stable levels in yield and income are reached which resulted in a high satisfaction and low uncertainty of farmers. As a result, only risk-aversive farmers with a high need satisfaction adopted the resistant variety in the model. These results suggest that when new resistant varieties are introduced to the market investments are probably needed to promote these to farmers and to increase their adoption. Interviews with conventional farmers showed that they do not consider late blight as a big problem because the application of fungicides leads to effective and cheap control (Chapter 2). These results support this finding. Secondly, to prevent emergence and spread of virulent strains additional management strategies are needed to increase durability of resistance. The development of sustainable crop protection systems therefore requires cooperation between actors in the whole sector to achieve structural transformations in disease control.

Further research

To simulate farmers' decision making we used the Consumat approach, a well-founded theory on human behaviour and previously used to simulate farmers' decision making. The implementation of the framework was supported by data from the literature on farmer behaviour and results from interviews with Dutch potato farmers. The model was able to reproduce patterns and trends observed in reality (e.g. boom-and-bust cycles) which supports the validity of the model framework (Grimm et al., 2005). However, different model structures at the micro-scale can lead to the same emergent patterns at the macro-scale (Schulze et al., 2017). Methods to validate processes on human behaviour include expert validation and role playing games (Ligtenberg et al., 2010). Secondly, alternative models of decision-making could be implemented to analyse the sensitivity of the results to different assumption of human decision making (Schlüter et al., 2017). These methods are important steps for further research.

Besides implementing alternative theories on human behaviour we identified some other relevant processes that could be implemented for further research. In the current model the landscape consisted of farmers that each manage one potato field while in reality farmers can have different fields spread over the farm. These potato fields can be managed in different ways and farmers usually grow a number of different potato varieties, also as a way of risk management. Secondly, in the model we included only one susceptible and one resistant variety. Currently, a number of different resistant varieties is available with resistance genes from different sources. More diversity in crop resistance can potentially reduce the risk on resistance breakdown and spread of virulent strains (Lof and Van der Werf, 2017; Mundt, 2014). Lastly, since potatoes are reproduced vegetatively by the use of seed potatoes it takes some time to increase the production of newly introduced potato varieties. The availability of seed potatoes can therefore constrain a rapid adoption of new resistant varieties. It would be interesting to implement these factors in the model to analyse the effect on the adoption of resistant varieties, the allocation of susceptible and resistant fields in the landscape and resistance durability.

In the model stakeholders such as breeding companies, the government and the market were represented as drivers of the system which influenced farmers' decision making. However, each of these stakeholders have their own objectives and interests which leads to various types of interactions such as competition, cooperation and trading (Chapter 2). Agent-based models are very suitable to include multiple types of agents and their interactions. As a next step, it would be interesting to explore the interactions between farmers, other stakeholders and late blight dynamics. With respect to the use of crop resistance in late blight control it would be mainly interesting to focus on the role of breeding companies and the effect of breeding and marketing strategies on late blight control.

4.5 Conclusion

In this paper we combined a framework on farmer behaviour to an epidemiological framework on potato late blight to explore the use of crop resistance in disease control. The framework on farmers' decision making was based on the Consumat approach and supported by data from literature on farmer behaviour and interviews with Dutch potato farmers. After introduction of a new resistant variety the model reproduced a so-called boom-and-bust cycle: the percentage of farmers growing the resistant variety increased (boom) until resistance breakdown occurred by emergence and spread of a virulent strain, and in response farmers switched to other potato varieties and management strategies (bust). By exploring the interactions between farmer behaviour and late blight dynamics the model increased insights in the factors and processes that could affect the adoption of a resistant potato variety and resistance durability. For example, a higher crop price and yield of the resistant variety increased the adoption by farmers. However, also a large number of farmers continued growing the susceptible variety with fungicides which suggests that cooperation in the whole potato sector is needed to achieve structural transformations in disease control. In addition, the high risk on resistance breakdown stresses the importance of resistance management strategies to increase resistance durability. It was found that emergence and spread of the virulent strain is the result of interactions between management strategies of farmers, the weather conditions and the allocation of potato varieties.

By exploring the social-ecological interactions related to disease control the model contributed to the field of social-ecological system research and agent-based modelling. The number of models that tackles two-way feedbacks between social and ecological systems is scarce, also due to the inherent complexity of such systems (Filatova et al., 2013; Parker et al., 2008; Schulze et al., 2017). This study provides a framework for linking decision-making processes of farmers to disease dynamics in an agent-based model. Implementing these two-way linkages allowed us to explore non-linear dynamics and feedback mechanisms within the social-ecological system. This approach could be useful for a whole range of systems focusing on management of emerging infectious diseases of crops.

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Appendix 4.A: Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Haverkort et al., 2008; Zwankhuizen and Zadoks, 2002). In the model description we focus on the processes related to farmers' decision-making. For more details on the epidemiological framework, we refer to Chapter 3.

4.A.1 Model purpose

The aim of the model is to simulate the interactions between farmers' decision making and late blight dynamics in an agricultural landscape with potato fields. The model is used to simulate the use of crop resistance in disease control by analysing the adoption of the resistant variety by farmers and the durability of resistance over time.

Table 4.6. Overview of late blight management strategies implemented in the model.

	Fungicide application	
Potato variety	**No**	**Yes**
Susceptible	Sus.-	Sus.+
Resistant	Res.-	Res.+

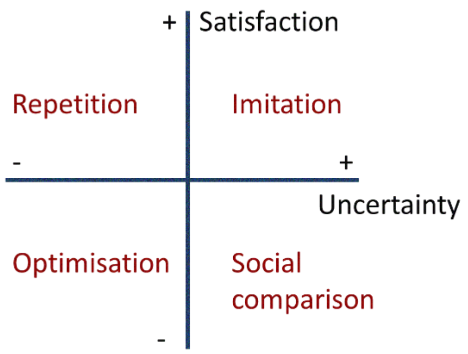

Figure 4.4. Overview of behavioural strategies in relation to farmers satisfaction and uncertainty according to the Consumat approach.

4.A.2 Entities, state variables and scales

The model includes three types of entities: farmers, grid cells and agricultural fields. The model represents an agricultural landscape of 10 x 10 km^2 and the grid cells are 200 × 200 m^2 (4 ha). The model is populated by farmers each of whom manages one potato field which consists of one or more grid cells. A network was initialised in which farmers are connected to the closest farmers around them (shortest distance) which represents a network of neighbours. An overview of farmer variables is shown in Table 4.7. For the state variables and model parameters related grid cells we refer to Tables 3.1 and 3.2.

In the model farmers select one of four late blight management strategies for their field (Table 4.6). Farmers can choose between a susceptible or late blight resistant potato variety with or without the use of fungicides. These strategies have different effects on field and landscape performance. Field performance was analysed for criteria including yield, income and infection level. To calculate farmers' income the crop price (p_m) was set at €13 per 100 kg^{-1} and the fungicide costs (f_c) at €50 per application. For the decision making processes we used behavioural strategies according to the Consumat approach (De Jong and De Snoo, 2002; Haverkort et al., 2008; Van der Werf, 1996). To evaluate their field performance farmers calculate the actual, estimated (predicted) and potential performance per criterion. These results are used to determine farmers satisfaction and uncertainty levels which leads to one of the following behavioural strategies: repeating, imitating, optimizing and social-comparison (Figure 4.4). The decision making process is influenced by personal characteristics including farmers need satisfaction and uncertainty tolerance level. We distinguish four farmer types in the model which differ in the weights assigned to the criteria (Table 4.1). Weights represent farmer preferences related to the criteria infection level, yield and income.

Processes on crop growth and disease dynamics are simulated at grid cell level. The grid cells are characterised by location, field number, potato variety (susceptible or resistant), fungicide use and variables and parameters for crop growth and late blight infection (see Tables 3.1 and 3.2). We consider only one type of susceptible and resistant variety (with one resistance gene). We assume the resistant variety has a 20% lower potential yield compared to the susceptible variety, which is reflected in the crop growth parameters. Two types of late blight are distinguished in the model: the wild-type and the virulent strain. The wild-type can only infect the susceptible variety, while a virulent strain can also infect the resistant variety. At the start of the simulation only the wild-type is present. The virulent strain can emerge during the growing season as the result of mutation. To simulate disease dispersal we used an aged-structured population model (Finckh et al., 2006). When spores germinate lesions first enter a latent phase of five days after which they become infectious and produce spores. After the infectious phase, lesions are added to the pool of no longer infectious tissue. A fraction of the produced spores is dispersed by wind to nearby cells where they can cause infections. Since late blight development and crop growth is weather dependant, we used measured weather data as input for the model.

Table 4.7. Overview of farmer variables.

Symbol	Description (unit)
FS	Field size (ha)
L	Network links (no)
F_t	Farmer type (-)
U_f	Uncertainty tolerance level (-)
S_f	Need satisfaction (-)
w_d	Weight of infection level criterion (-)
w_p	Weight of income criterion (-)
w_y	Weight of yield criterion (-)
BS	Behavioural strategy (-)
MS	Management strategy (-)
f_n	Fungicide applications (mean no year^{-1})
e_d	Estimated infection level (-)
e_p	Estimated income (€ ha^{-1})
e_y	Estimated yield (tonnes ha^{-1})
a_d	Actual infection level (-)
a_p	Actual income (€ ha^{-1})
a_y	Actual yield (tonnes ha^{-1})
p_d	Potential infection level (-)
p_p	Potential income (€ ha^{-1})
p_y	Potential yield (tonnes ha^{-1})
S_d	Infection level satisfaction (-)
S_p	Income satisfaction (-)
S_y	Yield satisfaction (-)
S_t	Total satisfaction (-)
U_d	Infection level uncertainty (-)
U_p	Income uncertainty (-)
U_y	Yield uncertainty (-)
U_t	Total uncertainty (-)

4.A.3 Process overview and scheduling

The time step in the model is one day and we simulate the potato growing season from May 1 to September 30 for 50 years. Processes in the model include (Figure 4.5): 1) Crop growth and disease dynamics (grid cells), 2) Update field performance (farmers), 3) Calculate relative satisfaction and uncertainty (farmers), 4) Select behavioural strategy (farmers), 5) Select management strategy (farmers) and 6) Predict field performance (farmers). Processes on crop growth and late blight dispersal are updated on a daily step. Decision-making processes of farmers (2 to 6) are executed at the end of the growing season. Within each submodel grid cells and agents are processed in a random order. A detailed description of model processes can be found in Section 4.A.7.

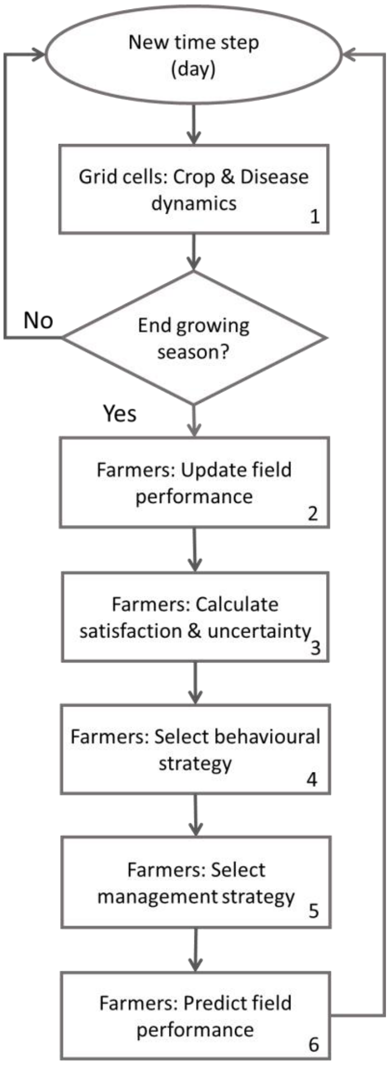

Figure 4.5. Flow chart of the model processes focussing on farmers' decision making.

4.A.4 Design concepts

Basic principles

The model is a spatial representation of the social-ecological system of potato late blight management. We focus on the interactions and feedbacks mechanisms between farmers' decision making and disease dynamics in an agricultural landscape. For the epidemiological processes we used the previously developed model (Chapter 3) and we added a social dimension of decision making on late blight control. The framework on farmers' decision making was based on the Consumat approach (Fry, 2008; Lammerts van Bueren et al., 2008) and results from interviews with Dutch potato farmers (Chapter 2).

Emergence
Both social and ecological dynamics are emerging from the model as a result of interactions between farmers' decision-making and disease dynamics including: farmers behavioural strategies, farmers late blight management strategies, field performance for the criteria infection level, yield and income and disease dispersal at landscape level.

Adaptation
During the simulation farmers can change their late blight management strategy. Four late blight management strategies are implemented in the model (Table 4.6). At the end of each year farmers analyse their field performance and based on the results for the criteria on infection level, yield and income their satisfaction and uncertainty is calculated. According to the Consumat approach one of four behavioural strategies is selected (Figure 4.4): repetition, imitation, social comparison and optimisation. Based on their behavioural strategy farmers continue using the same late blight management strategy or select one of the other three strategies (see Section 4.A.7 for more details).

Objectives
When farmers are unsatisfied and/or uncertain one of the following behavioural strategies is selected according to the Consumat approach: imitation, social comparison and optimisation. In the case of social comparison and optimisation farmers aim to select a management strategy that results in a higher satisfaction by improving their field performance related to the criteria infection level, yield and income.

Prediction
Based on observed results farmers predict their field performance (expected values) for the three criteria: infection level, yield and income. The expected values are calculated by taking the mean value using historical values of their own field of the last five years.

Sensing
Farmers can sense the field performance of the farmers in their network as well as their late blight management strategy. In the case of optimising behaviour farmers have information about the mean field performance per management strategy of the last growing season.

Interaction
Agents interact by sensing the state variables of other agents in their network. Secondly, the field performance of farmers is affected by the management strategies of other farmers in the landscape as a result of spatial interactions related to disease dispersal.

Stochasticity

At the start of the simulation the landscape is initialised in which farmers and potato fields are randomly allocated in the landscape. Management strategies are randomly divided over the farmers. Secondly, for a number of farmer characteristics the values are randomly selected to create a heterogeneous population including: the number of contacts (links), uncertainty tolerance level (0-1), need satisfaction (0-1) and farmer type. Farmer types differ in the weights which represent farmer preferences for the different criteria (Table 4.1). With respect to disease processes, at the start of each year the infection is initialised in a fraction of the potato grid cells, randomly selected. Weather data is used as input for the model and each year data of one year is selected from a dataset of 36 years. During the growing season spores are dispersed by wind and every time step the wind direction is randomly selected (northeast, southeast, southwest and northwest).

Collectives

Each field is a collective of one or more grid cells which is managed by a farmer. Farmers select a management strategy for their field and they evaluate their field performance by using the mean value of the grid cells belonging to the field.

Observation

At the end of each year data on landscape level was recorded including behavioural strategies and management strategies of farmers as well as variables related to disease dispersal in the landscape. Secondly the mean performance of each management strategy was calculated for the criteria infection level, yield and income. In the model interface several graphs are presented to observe the output over time.

4.A.5 Initialization

The model represents an agricultural landscape of 10 x 10 km^2 (50 x 50 grid cells) with a potato density of ±24%. At the start of the simulation the landscape is initialised with 350 farmers that each manage one potato field with a mean size of 7 ha. These parameters were derived from landscape data of a Dutch agricultural region. A network is initialised in which farmers are connected to the closest farmers around them, with a mean number of 5 links per farmers. At the start of the simulation we assume that all farmers grow a susceptible variety and the majority applies fungicides (90% of the farmers). Before the actual simulation started, the model was first run for five years without decision-making processes of farmers to create a list of reference values related to farmers field performance. An overview of initial values of crop growth and late blight can be found in Table 3.2. To create a heterogeneous population farmer characteristics were selected randomly (See Table 4.1 and Section 4.A.4 *Stochasticity*).

4.A.6 Input data

Meteorological data was used as input for the model to simulate crop growth and late blight dispersal during the growing season (May 1 to September 30). Data from two Dutch weather stations was used: Eelde (1981-1993) and Marknesse (1994-2016). In this way a dataset of 36 years of weather data was created. Mean daily temperature and total radiation was calculated and used to simulate crop growth. Secondly, based on calculation rules using hourly temperature and humidity during a 24-hour period, we determined if a day was suitable for sporangia to cause infection (NVWA, 2008). On a so-called 'blight day' newly produced spores can cause infections as a result of spore germination. See Chapter 3 (Section 3.2.1.6) for more details.

4.A.7 Submodels

Below the model procedures as shown in Figure 4.5 are described in more detail.

1. *Crop and disease dynamics (grid cells)*: At the start of each year late blight infections are initialised in a fraction of the potato fields, randomly selected. During the growing season (May till September), processes related to crop growth and disease dynamics are simulated with a daily time step. According to governmental regulations the potato haulm is destroyed when the disease severity in a field reaches 5%. As a result crop growth stops directly and the disease can no longer disperse to other fields. For a detailed description of these model processes we refer to Chapter 3 (Section 3.2.1.7).
2. *Update field performance (farmers):* At the end of each year the actual and potential field performance is determined for farmers for each performance criterion (i): infection level, yield and income.
   a. Actual field performance
      i. Yield (a_y): The mean potato yield is calculated (tonnes per ha) which is affected by the potato variety, weather conditions and infection with late blight.
      ii. Income (a_p): Income (€ ha^{-1}) is based on the actual yield and the price for potatoes minus costs for fungicide application (Equation 4.3). The crop price P_t is set at €13 per 100 kg^{-1}. This value was derived from a dataset on potato prices in the Netherlands from 2000 to 2017 (Rebaudo and Dangles, 2012). For the susceptible and resistant varieties the same value is used. Costs for fungicides are related to the mean number of applications (f_n) and the costs per application (f_c), set at €50.
      $$\boldsymbol{a_p = a_y * P_t * 10 - f_n * f_c} \quad (4.3)$$
      iii. Infection level (a_d): to analyse the infection level a scale from 1 to 4 was developed using results on disease severity (the percentage of

infected leaf tissue), where high values represent a high disease severity: 1: < 0.1%, 2: 0.1-1%, 3: 1-5%, 4: >5%.

b. The potential performance is the maximum result which could be achieved in a specific year without any losses caused by the disease.
   i. Potential yield (p_y) is determined by calculating the maximum yield that could be achieved for susceptible and resistant fields based on the weather conditions in that year (temperature and radiation).
   ii. The potential income (p_p) is calculated in the same way as the actual income but using the potential yield (Equation 4.4).
   $$\boldsymbol{p_p = p_y * P_t * 10 - f_n * f_c} \tag{4.4}$$
   iii. The potential infection level was set at 1 for all management strategies which represents no or a very low infection level.

3. *Calculate relative satisfaction and uncertainty (farmers):* Farmers calculate the relative uncertainty and satisfaction for each performance criterion (i). The overall uncertainty and satisfaction is influenced by the weights. Weights represent farmer preferences for the different criteria.
   a. Satisfaction is defined as the ratio between the actual field performance (a_i) and the potential field performance (p_i) for each performance criterion (i). The total satisfaction is based on the satisfaction level for each criterion and their weights (w_i) (Equation 4.5).
   $$\boldsymbol{S_t = \sum w_i a_i / p_i} \tag{4.5}$$
   b. Uncertainty is defined as the ratio between the actual field performance and the estimated value (e_i). The total uncertainty is based on the uncertainty for each criterion (i) influenced by the weights (Equation 4.6).
   $$\boldsymbol{U_t = \sum w_i a_i / e_i} \tag{4.6}$$
4. *Select behavioural strategy (farmers):* Farmers compare their relative satisfaction and uncertainty level (S_t and U_t) to their personal need satisfaction (S_f) and uncertainty tolerance level (U_f). Based on the Consumat framework farmers select one of four behavioural strategies (Figure 4.4):
   a. If unsatisfied and uncertain ($S_t < S_f$ and $U_t < U_f$): Social comparison
   b. If unsatisfied and certain ($S_t < S_f$ and $U_t > U_f$): Optimisation
   c. If satisfied and uncertain ($S_t > S_f$ and $U_t < U_f$): Imitation
   d. If satisfied and certain ($S_t > S_f$ and $U_t > U_f$): Repetition
5. *Select management strategy (farmers):* According to their behavioural strategy farmers select a management strategy.
   a. Social comparison: Farmers select the criterion they want to improve: infection level, yield or income. Therefore farmers compare the results of their field for each performance criterion (i) by calculating the weighted satisfaction (O_i) which is based on the satisfaction level and the weights) (Equation 4.7).
   $$\boldsymbol{O_i = S_i(1 - w_i)} \tag{4.7}$$

The criterion with the lowest score is selected by farmers which represents the criterion they want to optimize. For this criterion, farmers compare the performance of the other farmers in their network and take over the management strategy of the farmer with the best result.

b. Optimisation: Farmers select the criterion they want to optimize similar to social comparison. Farmers compare the mean performance of all four management strategies based on the results of the previous year and adopt the management strategy that has the best result for the criterion the farmer wants to optimize. If management strategies were not used by farmers the results of the previous year are used. Since the management strategies including the resistant variety with and without fungicides are not used by farmers at the start of the simulation, the potential values are used which represents the mean field performance of these two strategies. When the resistant variety with and without fungicides have the same highest score it is assumed that farmers select the resistant variety without fungicides.
c. Imitation: Farmers adopt the management strategy which is used by the majority of farmers in their network. If this includes two or more strategies one of these strategies is randomly selected.
d. Repetition: Farmers don't change their management strategy.

6. *Predict field performance (farmers):* Farmers estimate the value (e_i) for each performance criterion (i) for the coming year. Therefore they calculate the mean value using historical values of their own field of the last five years.

Chapter 5

Moving perceptions on potato late blight control: workshops with model-based scenarios

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Under review

Abstract
Late blight caused by *Phytophthora infestans* is one of the main diseases in potato production. The Netherlands has a high potato density and favourable weather conditions for the disease, and this combination leads to frequent outbreaks of late blight. A previously developed spatially explicit agent-based model of the host-pathogen system was adapted and used in workshops with conventional and organic farmers to demonstrate and discuss the potential role of resistant varieties for effective and sustainable control of late blight. The model represents an agricultural landscape with potato fields that are managed by farmers. In the model we consider a susceptible variety and a resistant variety with a single-resistance gene. We presented model-based scenarios and used qualitative and quantitative measures to analyse the effect of the workshop on farmers' perception on late blight control. The scenarios simulated effects of farmer decisions regarding the use of crop resistance and fungicide application on disease control at the landscape level over a period of ten years. The model showed that growing a resistant variety can reduce disease incidence in the landscape, however, after a couple of years resistance breakdown occurs by emergence of a new virulent *P. infestans* strain. If no countermeasures were taken the new virulent population could spread fast through the landscape, reducing potato yield of resistant fields. The model showed a number of resistance management strategies that could be effective to increase resistance durability including (reduced) use of fungicides on all susceptible or all resistant fields, growing a resistant variety with multiple resistance genes (instead of single-gene) and immediate haulm destruction of resistant fields after infection with the virulent strain. The workshop was very useful to analyse changes in farmer perceptions. Before the workshop many farmers were not aware that resistance breakdown could occur. After the workshop a large majority of the farmers agreed that stakeholders need to cooperate for effective and sustainable late blight control. By analysing the disease dynamics at the landscape level, the model showed the importance of collective action. For conventional and organic farmers similar changes in perception were observed for almost all topics, showing that the workshop contributed to a common understanding on late blight control. The majority of farmers were very positive about the workshop. They stated that they found the model reliable, that interesting scenarios were presented and that their understanding of the effect of management strategies on disease control had improved. We conclude that the use of model-based scenarios in workshops was very useful to increase farmers' knowledge of the system and served as a good starting point for discussions among actors facing the complex problems of late blight control and potato resistance management.

Keywords: Agent-based modelling, participatory modelling, social-ecological systems, cropping patterns, host-pathogen interactions

5.1 Introduction

Late blight caused by *Phytophthora infestans* is one of the main diseases in potato production. The Netherlands has a high potato density and in combination with favourable weather conditions, frequently experiences outbreaks of the disease. In conventional farming the use of fungicides is the prevailing method in the control of late blight, but this involves high costs and the fungicides are harmful for the environment (Haverkort et al., 2008). Since organic farmers are not allowed to use chemicals in disease control, yields can be dramatically low in years with early outbreaks of the disease. In contrast to other European countries the use of copper as fungicide is not permitted in organic farming in the Netherlands. Besides, the Dutch national regulation on late blight management obliges farmers to destroy the haulm at 5% infestation. The development of resistant varieties can play a key role in sustainable control of the disease by reducing the amount of fungicides in conventional systems and improving disease management for organic farmers (Finckh et al., 2006).

In a previous model study we analysed the potential and risks related to the use of late blight resistant varieties in disease control (Chapter 3). A spatially explicit agent-based model was developed to simulate disease dynamics at landscape level. The model showed that increasing the fraction of fields with a resistant variety (with a single resistance gene) strongly reduced late blight severity. Secondly, growing a resistant variety could be very beneficial for organic farmers since in most years yields were higher compared to susceptible fields without fungicides. However, the model also showed that resistance breakdown could occur as a result of emergence of a new virulent *P. infestans* strain. When no countermeasures were taken the virulent strain could spread through the landscape and establish itself in the population. As a result the resistance would become less effective each year, decreasing mean potato yield from fields with a resistant variety. This is also known from practical experience when new virulent strains emerged that could overcome resistance after the introduction of single-gene resistant potato varieties (Fry, 2008).

Farmers play a key role in the control of late blight since they make decisions on crop management which directly affect spread of the disease (Chapter 2). Since the disease is dispersed by wind, farmers are also affected by the management strategies of other farmers in the landscape. Fields of farmers without effective disease control can therefore act as sources of infection. Especially with respect to the use of resistant varieties it is important to keep disease severity low to prevent the emergence of new virulent strains. A model showing disease dynamics at landscape level can be helpful to show the consequences of individual actions at larger spatial and temporal scales. Previous results showed that decisions on late blight management were influenced by economic incentives which includes a trade-off between reducing management costs and limiting the risk of disease damage (Chapter 2). Therefore, it is important that farmers can assess the effect of management strategies and late blight dynamics to make informed decisions.

In this paper we used a modified version of the previously developed agent-based model as a learning tool in workshops with farmers. Participatory modelling has been recognised as a powerful tool to increase stakeholders knowledge of the system (Voinov and Bousquet, 2010). For example Speelman and García-Barrios (2010) showed that an agent-based model on crop-pest interactions was useful to facilitate learning and increase understanding on the dynamics of land-use and farming systems. By analysing model scenarios the participants can explore social-ecological feedbacks and potential surprises (Oteros-Rozas et al., 2015). Secondly, simulation tools are useful to show the effect of multiple agents on the system dynamics which can serve as a starting point for discussion among participants (Chaturvedi et al., 2014; Cleland et al., 2012). By interactions with and between stakeholders learning on the system is taking place (Barreteau, 2003). Furthermore, exchanging points of view can help stakeholders to find common ground and reach consensus and in this way support collective decision-making processes. To evaluate the learning process surveys and questionnaires can be used (Voinov and Bousquet, 2010). Knowledge acquisition can be evaluated by using pregame and postgame surveys in combination with self-reporting by participants (Mayer et al., 2014).

We presented model-based scenarios to groups of farmers and after discussions applied qualitative and quantitative measures to analyse the effect of the workshop on farmers' perceptions on late blight control. Several model scenarios were developed in which we compared the use of fungicides and crop resistance in disease control. Besides showing the potential and risks for potato production as related to the use of crop resistance, also several resistance management strategies aiming to increase resistance durability were analysed. In the workshop we showed disease dynamics at landscape level over longer time periods and analysed changes in farmers' perception on late blight control. Because conventional and organic farmers strongly differ in farm and late blight management we organised workshops with both types of farmers and compared their perception on late blight control. Below we first give a short description of the model and the scenarios, followed by the setup of the workshops. Thereafter we present the outcomes of the model as well as the results of the workshops.

5.2 Methods

A previously developed spatially explicit agent-based model (Chapter 3) was adapted and used in workshop with farmers. The model represents an agricultural landscape with potato fields. The processes in the model include crop growth and disease dynamics affected by weather conditions. The model was used to present several scenarios related to the use of crop resistance and fungicide application in disease control. A try-out session was organised with two organic potato growers to improve the setup of the workshop.

5.2.1 Model description

The model represents an agricultural landscape (10 x 10 km^2) with potato fields that are managed by farmers (Figure 5.1). The model consists of grid cells which represent an area of 200 x 200 m^2 (4 ha) that are clustered in agricultural fields. The potato density in the landscape is set at 24% and the mean field size at 7 ha. These parameters were derived from landscape data of an agricultural region dominated by arable cropping in the Netherlands (Noordoostpolder). At the initialization of the model potato fields are randomly distributed in the landscape. Crop rotation is not included in the model. Farmers grow a susceptible or late blight resistant variety on their field (referred to as susceptible and resistant fields) with or without the use of fungicides. In the model we consider only one susceptible and one resistant potato variety, the latter with a single-resistance gene. To simulate crop growth we use equations for leaf area development and tuber growth (Skelsey et al., 2009b). We assume that the resistant variety has a 20% lower potential potato yield than the susceptible variety which is reflected in the crop growth parameters. This is also the case for late blight resistant potato varieties currently available on the market; however, the yield potential may increase in the near future with the introduction of new resistant varieties.

In case fungicides are applied on susceptible fields weekly application is assumed starting at the day of crop emergence. Protective fungicides are used and when the disease severity in a field reaches 1% farmers switch to curative fungicides. On resistant fields we assume that less frequent use of fungicides is sufficient to prevent infection. So instead of weekly application, the moment of fungicide application is delayed with one day on ‘non-blight days’ (see below). In reality, farmers can use decision-support systems to optimize the timing of fungicide application (Wharton et al., 2008).

In the model we distinguish two *P. infestans* populations: the wild-type and a virulent strain. The wild-type can infect the susceptible potato variety while the virulent strain can also infect the resistant variety. At the start of the simulation only the wild-type is present and the virulent strain can emerge as a result of mutation during spore production of the wild-type. To simulate disease dispersal of both populations we use an aged-structured population model (Skelsey et al., 2010). When spores germinate they first enter a latent phase of five days after which they become infectious and produce spores. Afterwards infectious lesions are added to the pool of no longer infectious tissue. A fraction of the produced spores is dispersed by wind to neighboring fields where they can cause infection. Spores are dispersed up to a distance of 1000 m from the infected patch. When the total disease severity in a grid cell reaches 5% the potato haulm is destroyed according to Dutch governmental regulations (NVWA, 2008). As a result, crop growth and disease dispersal stop directly and the field can no longer act as a source of infection.

Since crop growth and disease dispersal is affected by the weather conditions we used measured weather data as input for the model. Mean daily temperature and total radiation was calculated and used to simulate crop growth. Secondly, based on calculation rules using hourly temperature and relative humidity during a 24-hour period, we determined if a day was suitable for sporangia to cause infection (Skelsey et al., 2009a). On a so-called 'blight day' newly produced spores can cause infections as a result of spore germination. Expansion of existing lesions also occurs on 'non-blight days'.

The time step of the model is one day and we simulated growing seasons from May 1 to September 30 (153 days) for 10 years. At the start of each year variables are reset and initial infections are initialised in randomly selected potato fields, but the ratio between the wild type and the virulent strain is maintained. At the end of each year larger scale, aggregate variables were calculated from individual cell data on potato yield and late blight infection (see Section 5.2.2). For a detailed description of the model and an overview of model variables and parameters we refer to Chapter 3 (Section 3.2.1).

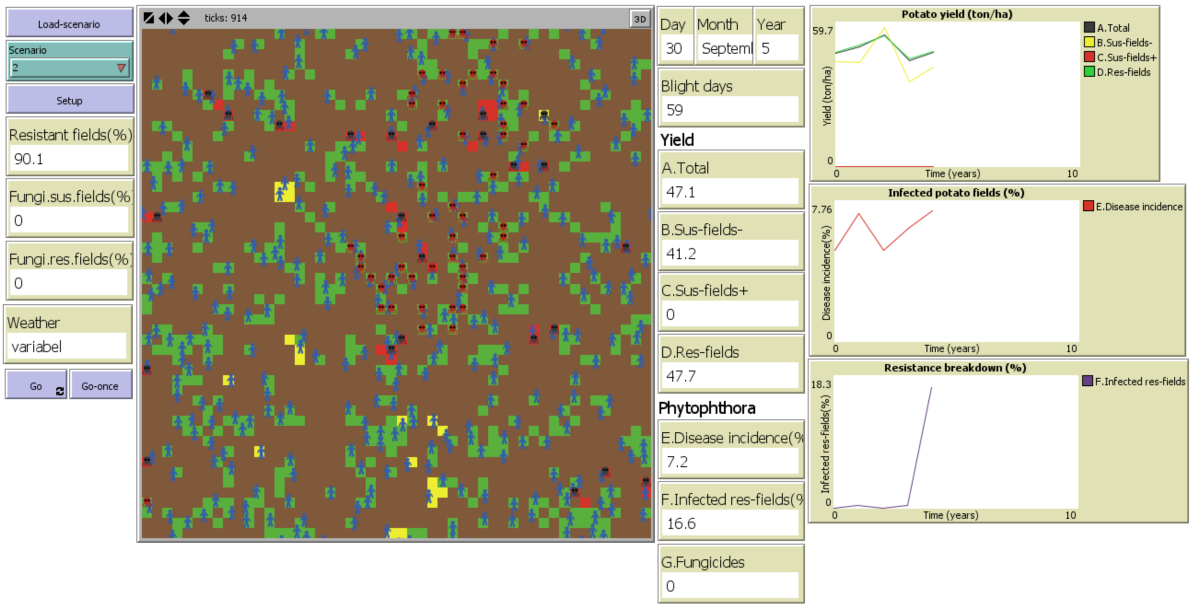

Figure 5.1. The model interface used in the workshop with an example of Scenario 2 (see Section 5.2.2). Information on the scenario is shown on the left, the agricultural landscape is shown in the middle and model output on the right.

5.2.2 Model scenarios

Scenarios were developed and presented in the workshop to show the effect of management strategies on disease control at landscape level (Table 5.1). In these scenarios we focussed on the use of fungicide application and crop resistance in the control of potato late blight. We varied the fraction of potato fields with the resistant and susceptible potato variety, referred to as the fraction resistant and susceptible fields. According to Carpenter et al. (2006) scenario analysis has the largest power when exploring a small set of scenarios that show clear and striking difference. In addition, since time during the workshop is limited it is better to focus on scenarios which, according to the research team, will have the greatest impact on the results or scenarios that are easily to implement (Voinov and Bousquet, 2010). By showing scenarios that deviate considerably from the current situation stakeholders are challenged to think outside the box as well as about the goals they want to accomplish and how these can be reached. Presenting feasible scenarios given existing system characteristics and management practices is useful to discuss the strategies that could be implemented on the short-term. Taking these aspects into account seven scenarios were developed.

Scenario 1 was very close to the actual cultivation practices in the Netherlands in which the application of fungicides is the dominant strategy in disease control. No late blight resistant varieties were grown, which has been the case for a long time. To simulate the presence of organic potato growers, a small fraction of the potato fields was not protected by fungicides.

Secondly, to show the potential and risks of crop resistance in disease control Scenario 2 was developed where a resistant variety was grown on 90% of the potato fields. No fungicides were used, also not on the susceptible fields. The purpose of presenting Scenarios 1 and 2 was to show the participants differences between two opposite scenarios of the use of fungicides and crop resistance in disease control.

Scenario 3 represented an intermediate situation with a small fraction of resistant fields and the majority of farmers using fungicides on susceptible fields. This scenario was used to analyse several resistance management strategies which were derived from literature including: 3.1) Fungicide application on all susceptible fields in line with the conventional way of disease suppression, 3.2) Fungicide application on all resistant fields for additional protection, 3.3) Clustering of resistant fields in the landscape to create spatial barriers for disease spread, 3.4) Haulm destruction immediately after infections with the virulent strain in resistant fields (instead of the 5% threshold) to avoid spread of the new virulent strain, 3.5) Growing a potato variety with multiple resistance genes (instead of a single gene) to reduce the probability of resistance breakthrough. In this case late blight strains need two mutations to overcome two resistance genes and therefore the mutation fraction was squared in this scenario. In Scenario 3.3 resistant fields were clustered in groups of ten resistant fields instead of random allocation of the resistant fields as applied in the other scenarios.

The model output we presented consisted of the potato yield and variables related to spread of late blight infections: 1) potato yield (tonnes/ha), 2) disease incidence: the percentage of infected potato grid cells with a disease severity ≥ 1% (Skelsey et al., 2010) and 3) infected resistant fields: the percentage of resistant potato grid cells in the landscape infected with the virulent strain as a measure to analyse resistance breakdown. Moreover, the mean number of fungicide applications per ha was shown for the whole landscape. For every scenario the model was run for 10 years.

Table 5.1. Overview of scenarios analysed with the model and presented in the workshops. Potato fields are characterized by percentages of each potato variety (susceptible and resistant fields) and of fields receiving application of fungicides (yes/no). These settings were varied per scenario and for scenarios 3.3-3.5 additional practices were implemented.

Scenario			Potato variety (%)		Fungicide application (%)	
No	Name	Description	Susceptible fields	Resistant fields	Susceptible fields	Resistant fields
1	Fungicide application	Disease control by fungicide application in a landscape with susceptible fields	100	0	90	0
2	Crop resistance	Disease control by crop resistance: a landscape with mainly resistant fields	10	90	0	0
Scenarios resistance management:						
3.0	Baseline	A small fraction of resistant fields and most susceptible fields protected by fungicides	90	10	90	0
3.1	Fungicides susceptible fields	Fungicide application on all susceptible fields	90	10	100	0
3.2	Fungicides resistant fields	Fungicide application on all resistant fields	90	10	90	100
3.3	Clustering	Clustering of resistant fields in the landscape	90	10	90	0
3.4	Haulm destruction	Immediate haulm destruction after infection in resistant fields	90	10	90	0
3.5	Multiple resistance genes	Resistant variety with multiple resistance genes	90	10	90	0

Table 5.2. Overview of characteristics of farmers who attended the workshop sessions.

Session	Partici-pants (no)	Type	Province	Potato type	Mean age	Mean farm size (ha)	Mean potato area (ha)
1	8	Organic	Groningen	Mainly seed potatoes, some ware potatoes	40	68	13
2	12	Organic	Flevoland	Mainly ware potatoes, some seed potatoes	47	*53	7
3	15	Organic	Zeeland	Mainly ware potatoes, some seed potatoes	46	100	13
4	6	Conventional	Zeeland	Ware potatoes	52	123	50
5	10	Conventional	Zeeland	Mainly ware potatoes, some seed potatoes	49	71	23

*Data of two participants was left out since they were part of a large farmer cooperative with ±1800 ha of land.

5.2.3 Workshop setup

In total five workshops were carried out with three groups of organic and two groups of conventional farmers (Table 5.2). The workshop started with a presentation describing the model and the main model processes. Secondly, the model scenarios were presented. As a result of stochastic processes, the model showed variation in model output between simulation runs. For each scenario one representative run was selected which was used in all the workshops so the results of the sessions could be easily compared. A workshop session took on average about three hours.

During the workshops, several types of data were collected. This included general information of the participants such as age, location, farm size, potato varieties and late blight management strategies. To test a priori knowledge we analysed participants' expectations on model output variables before each scenario using multiple choice questions. After showing the model results of each scenario the outcomes were discussed and participants were asked to reflect on the results. Furthermore, participants were asked to rate the same statements (5-point Likert scale) on late blight management before and after the workshop to analyse changes in their perception. In a group discussion afterwards the model results and implications were discussed to collect qualitative data. Secondly, an evaluation form was handed out at the end of the workshop (5-point Likert scale) to get feedback on the setup of the workshop and to measure participants' self-reported learning. During each workshop session notes were taken by an observer and all workshops sessions were recorded for later analysis.

5.2.4 Statistical analysis

During the workshops data was collected with questionnaires using a 5-point Likert scale and multiple-choice answers. We analysed differences between conventional and organic farmers as well as differences before and after the workshop. All data were imported into the programme SPSS Statistics 23 for Windows. We used a Mann-

Whitney U test to analyse data with an ordinal scale (including Likert data), and a Chi-Squared test for multiple choice answers with a nominal scale. Exact significant values were calculated because of small sample sizes. For visualisation of Likert scale data r-packages were used (http://www.bryer.org/project/likert/).

5.3 Results

5.3.1 Model scenarios

The model output variables were presented in the workshop sessions for the scenarios described in Table 5.1 (Figures 5.2 and 5.3). When comparing the effect of management strategies on disease control the model showed that in Scenario 1 (Fungicide application) the susceptible fields with fungicide application reached relative high yield levels. Potato yield of susceptible fields not protected by fungicides was highly variable, as affected by the severity of late blight infection which depended on the number and timing of blight days per year. Disease incidence at landscape level ranged between 20% and 70% showing that fungicides would not prevent spread of the disease but suppress the disease so that acceptable yield levels were achieved (Figures 5.2a and 5.2d). The high disease incidence was also the result of the relatively large number of initial infections which could develop in susceptible fields.

In Scenario 2 (Crop resistance), the disease incidence was very low and potato yield was high in the first years (Figures 5.2b and 5.2e). Because we assumed that the resistant variety has a lower potential yield, resistant fields reached a lower yield compared to the susceptible fields treated with fungicides in Scenario 1. Susceptible fields not protected by fungicides had a higher yield level compared to the first scenario as a result of the low disease incidence in the first years. However, after four years infections in resistant fields were observed by emergence of a new virulent strain. Because the resistant variety was grown on the majority of potato fields, no fungicides were used and no countermeasures were taken, the new virulent population could spread fast through the landscape (Figure 5.2h). As a result, the disease incidence rapidly increased, decreasing potato yield of both resistant and susceptible fields. The yield of resistant fields eventually dropped below the yield of susceptible fields when all resistant fields were infected.

Scenario 3 (Baseline) showed similar trends. Susceptible fields protected by fungicides had the highest potato yield, followed by resistant fields and susceptible fields without fungicide application (Figure 5.2c). Although in this scenario the fraction of resistant fields was lower, resistance was overcome and the virulent strain would establish in the population. Compared to Scenario 2 this process was slower because of the lower number of resistant fields.

Scenario 3 was used to analyse the effectiveness of resistance management strategies (Figure 5.3). It was found that resistant fields were not infected when fungicides were applied to all susceptible fields (Scenario 3.1) or all resistant fields (Scenario 3.2). In Scenario 3.1 (Fungicides susceptible fields) the disease would be successfully suppressed so the virulent population stayed very small and could not infect the resistant fields. In Scenario 3.2 (Fungicides resistant fields) resistant fields were protected by fungicides preventing infection and spread of the virulent strain. Using a resistant variety with two resistance genes (stacking) instead of a single-gene resistant variety was also a successful strategy to increase resistance durability (Scenario 3.5). The chance that a virulent strain emerges that can infect this variety was very small and did not occur in the model. Immediate haulm destruction of resistant fields after infection (Scenario 3.4) stopped spread of the virulent strain. The number of infected resistant fields stayed very small and establishment of the virulent strain could be prevented. The only strategy that was not effective was the spatial clustering of resistant fields in the landscape (Scenario 3.3). Clustering of resistant fields in the landscape reduced the risk of virulent strain spread to these fields since they emerge in infected susceptible fields. However, once virulent spores reached a resistant field the virulent strain could spread fast within the cluster of resistant fields. As a result, the virulent strain established in the population and the percentage of infected resistant fields increased rapidly over time.

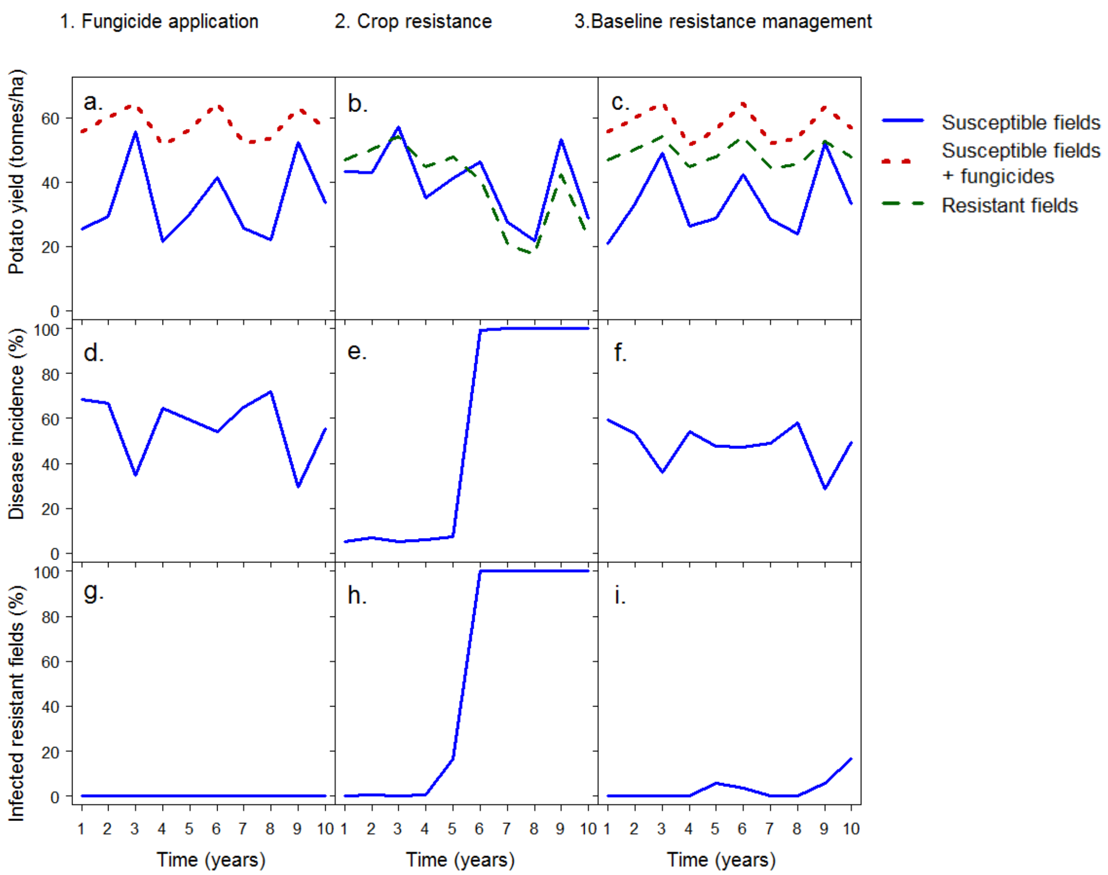

Figure 5.2. Model results presented in the workshops (scenarios 1-3.0 described in Table 1). Three different output variables are shown over a time period of ten years: potato yield (tonnes fresh yield/ha), disease incidences (the percentage of potato grid cells with a disease severity>1%) and infected resistant fields (%) to analyse resistance breakdown. Since Scenario 1 only includes susceptible fields the percentage of infected resistant fields is zero in plot g.

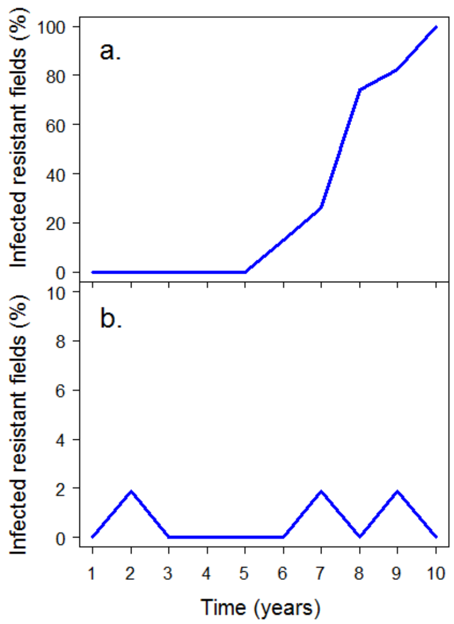

Figure 5.3. Model results presented in the workshops for a) Scenario 3.3 (Clustering) and b) Scenario 3.4 (Haulm destruction) (see Table 5.1). Of these resistance management strategies only the effect on the percentage of infected resistant fields is presented here. Note different scales on the Y-axes.

5.3.2 Workshop results

5.3.2.1 Prior understanding of management strategies and model processes

Before each scenario was presented to the participants, they were asked to answer multiple choice questions on model output variables related to their understanding of management strategies and model processes. Organic and conventional farmers had different expectations with respect to potato yield (Table 5.3). For example, in Scenario 2 (Crop resistance) 57.1% of the organic farmers expected a high yield of resistant fields compared to 18.8% of the conventional farmers. This is understandable, since in practice resistant varieties can be much more beneficial for organic farmers in years with high disease pressure. Organic farmers were more optimistic about the effectiveness of crop resistance in disease control. In Scenario 2, 53.6% of the organic farmers expected a low disease incidence compared to 31.1% of the conventional farmers. Furthermore, the results showed differences in understanding of resistance breakdown. In Scenario 2, 20% of conventional farmers indicated they did not know whether resistance breakdown would occur compared to 3.7% of organic farmers. In Scenario 3.0, 45,5% and 56.3% of the conventional and organic farmers, respectively, expected resistance breakdown would occur which showed the diversity in understanding of this complex concept.

Conventional and organic farmers had a different perception on the effectiveness of resistance management strategies (Figure 5.4). Both farmer types expected that growing resistant varieties with multiple resistance genes would be the most effective approach and that clustering of resistant fields in the landscape would be less effective. The second-best strategy according to organic farmers would be immediate haulm destruction, compared to fungicide application on susceptible fields for conventional farmers. This reflects their opinion and current use of management strategies in disease control.

Table 5.3. Farmers' answers to multiple choice questions related to expected outcomes of model output variables before the results of each scenario were presented. The questions relate to relevant model output variables in scenario 1, 2 and 3.0 (see Table 5.1).

Questions per scenario	Farmer type (N)	Response (%)			
		I don't know	Low	Average	High
What outcome do you expect for the following model output variables in scenario 1 (1a-1c) and 2 (2a-2d)?					
1a. Yield susceptible fields	Conventional (16)	0.0	93.8	6.6	0.0
	Organic (27)	0.0	77.8	18.5	3.7
1b. Yield susceptible fields + fungicides	Conventional (16)	0.0	0.0	50.0	50.0
	Organic (27)	0.0	0.0	14.8	85.2
1c. Disease incidence	Conventional (15)	0.0	6.7	33.3	60.0
	Organic (27)	3.7	25.9	48.1	22.2
2a. Yield susceptible fields	Conventional (16)	0.0	68.8	31.3	0.0
	Organic (28)	3.6	35.7	53.6	7.1
2b. Yield resistant fields	Conventional (16)	0.0	12.5	68.8	18.8
	Organic (28)	0.0	0.0	42.9	57.1
2c. Disease incidence	Conventional (16)	0.0	31.3	62.5	6.3
	Organic (28)	0.0	53.6	25.0	21.4
2d. Infected resistant fields	Conventional (15)	20.0	0.0	53.3	26.7
	Organic (27)	3.7	37.0	40.7	18.5
		I don't know	No	Yes	
3. Do you think resistance breakdown will occur in scenario 3.0?	Conventional (16)	18.8	25.0	56.3	
	Organic (33)	21.2	33.3	45.5	

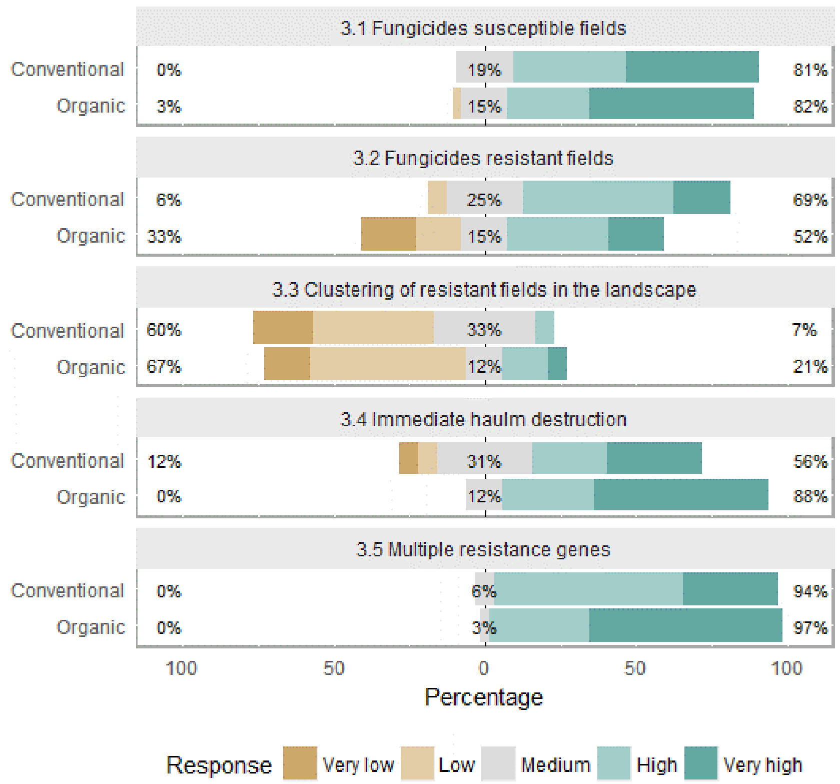

Figure 5.4. The percentage of farmers expecting a different degree of effectiveness (from very low to very high) of resistance management strategies analysed with the model (Scenarios 3.1-3.5, see Table 5.1). Farmers had to rate these strategies before model results were shown.

5.3.2.2 Discussing the model results

Farmers were surprised by the relatively high disease incidence in Scenario 1. Despite the frequent fungicide applications, the disease could spread fast through the susceptible fields resulting in high disease pressure. Conventional farmers mentioned that in practice, in periods of favourable weather conditions for disease spread adaptive spraying schedules are adopted (with more frequent fungicide applications) to effectively suppress the disease. This process could be added in the model which could reduce the disease incidence. Secondly, organic farmers remarked that yield of susceptible fields without fungicide application was relatively high compared to their own experiences. It was discussed that the model is a simplification of the system and other yield limiting factors (except for late blight infection) were not included in the model. Therefore, the model should be used to identify trends rather than to generate exact predictions. This also relates to the results on resistance breakdown in Scenarios 2 and 3. It was discussed that the model can increase understanding of the processes that affect resistance breakdown but cannot be used to make predictions after how many years resistance breakdown will occur.

In Scenario 2 many farmers did not anticipate that resistance breakdown could occur already after a couple of years and that the percentage of infected resistant fields increased very fast over time. One farmer expressed this observation as follows: '*As soon as the resistant fields get infected they are doomed'*. Secondly, conventional farmers were surprised that during the first years of the simulation the disease incidence was very low as a result of the high fraction of resistant fields (before resistance breakdown occurred). For example, one farmer mentioned that susceptible fields will always get infected, even when they are surrounded by resistant fields.

Although the model showed resistance breakdown in Scenario 2, many farmers did not expect it would also occur in Scenario 3.0, with a lower fraction of resistant fields. With respect to resistance management strategies farmers had not expected that the use of fungicides on resistant fields was effective to increase resistance durability. After discussing the outcomes of the model also the practical implications of the proposed resistance management strategies were highlighted. The use of potato varieties with multiple resistance genes was considered the best option for resistance management; however, farmers are dependent on breeding companies to develop these varieties. Secondly, since chemical control is not allowed in Dutch organic farming the use of fungicides for resistance management is currently not possible for organic farmers. If new, organic fungicides would become available in the future these might be considered in late blight control. For Scenario 3.4 (Haulm destruction) it would be very important that all farmers cooperate so the virulent strain does not get a chance to further develop and establish. This can be risky when not all farmers are equally committed to check for infections in resistant fields. In case of an infection they have to destroy the haulm immediately and put the long-term common interest of maintaining resistance durability above their personal short-term interest of attaining high yield levels. Some of the organic and conventional farmers felt that an inspection is needed so all farmers follow these rules. Overall, organic farmers agreed that until varieties with multiple resistance genes are available it is very important to increase resistance durability of single-gene varieties by immediate haulm destruction. Conventional farmers stressed that fungicides should be used in resistance management. For example one farmer stated that *'All potato fields should be sprayed, to greater or lesser extent'*. Another option proposed by conventional farmers was that all organic farmers grow resistant varieties and all conventional farmers apply fungicides on susceptible and resistant varieties.

5.3.2.3 Changes in perception

Farmer perception on late blight control before and after the workshop is shown in Figure 5.5 (statements a to j). For organic farmers, perceptions after the workshop were significantly different than before the sessions. Changes were observed for conventional farmers but these were not significant. For organic farmers significant differences were found for five statements (b, c, e, h and j) showing a strong effect of the workshop. After the workshop organic farmers were more positive about the use of fungicides in disease control (statement b, P=0.049), probably because the model showed they can be used effectively for resistance management. In contrast, after the workshop organic farmers were less positive about the use of crop resistance in disease control (statement c, P=0.023). This also relates to increased awareness on the risk on resistance breakdown (statement e, P=0.038). Although not significant, after the workshop more farmers (organic and conventional) agreed that additional resistance management strategies could increase resistance durability. Statement h posed that farmers are responsible for late blight control on their own farm and after the workshop organic farmers more agreed to this statement (P=0.013). This reflects increased awareness that all farmers have to contribute to disease control. Although more organic farmers agreed that cooperation is needed for effective control (statement g, not significant), they also felt that it is more difficult to realise (statement j, P=0.024).

In contrast, after the workshop conventional farmers thought that collaboration with other farmers and stakeholders on late blight control is less difficult (statement j). Based on the discussions this can be related to the implementation of resistance management strategies. Organic farmers doubted how realistic it is to assume that all farmers will commit themselves to disease resistance management when it would imply early haulm destruction and thus yield loss. The model also showed that fungicides can be used effectively for resistance management which is in line with current practices of conventional farmers.

With respect to prior perception a significant difference between conventional and organic farmers was found for statement d that crop resistance should be used for more environmental friendly control of potato late blight (P=0.003). Organic farmers agreed more to this statement than conventional farmers, which reflects their ideas about farm management and the environment. Secondly, these groups had a different perception on statement e on the risk on resistance breakdown (P=0.019). About 75% of conventional farmers expected that resistance would be broken compared to 35% of organic farmers. Lastly, a difference was found between conventional and organic farmers concerning the understanding that farmers need to cooperate in the control of late blight (statement g, P=0.002; 44% vs 82% respectively agreed to this statement). After the workshop, organic and conventional farmers still differed on statement g, but not on the other statements.

5.3.2.4 Workshop evaluation

Overall, farmers were quite positive about the model and the representation of the processes (Figure 5.6, statements a to f). Farmers mentioned that the model is very theoretical but they recognized the patterns that emerged from the model. The omitted processes were discussed with the farmers. A number of management strategies were mentioned which could affect late blight severity such as pre-sprouting, soil fertilisation, growing early maturing potato varieties, adaptive spraying regimes and the type of fungicides used. Secondly, farmers were missing processes related to tuber infection and its effect on yield, which was not included in the model as only foliar infestation was considered.

Almost all farmers agreed (statements e and f) that the model was educational (93%) and the scenarios presented were interesting (96%). Statements that supported this include: '*The model pushes you to face the facts*' and '*Some interesting topics came up which we can discuss*'. Some farmers referred to the model as a 'black box', or 'computer game', but the majority did not experience the model as complicated (statement d, 60% and 79%). Organic farmers found the scenarios presented more interesting (statement f) compared to conventional farmers (P=0.010). Organic farmers were more interested to see the model results for alternative scenarios not presented in the workshop (statement i) compared to conventional farmers (59% vs 23%, P=0.037). Organic farmers would like to see model scenarios with smaller fractions of resistant fields, a lower potato density, more diversity in resistant potato varieties (with different resistance genes), intercropping practices with potato varieties and seed potato production.

Regarding statement g, the majority of organic farmers confirmed that during the workshop they gained new insights on late blight control (58%). Conventional farmers were less positive (33%) but this difference was not significant. Farmers mentioned they learnt more about resistance breakdown and resistance management. Both groups of farmers learnt about the effect of management strategies on disease control (statement h, 67% vs 62%). Farmer quotes that support this include '*Resistance breakdown can occur easily when no measures are taken*' and '*It is dangerous to grow varieties with only one resistance gene, but crop resistance offers opportunities*'.

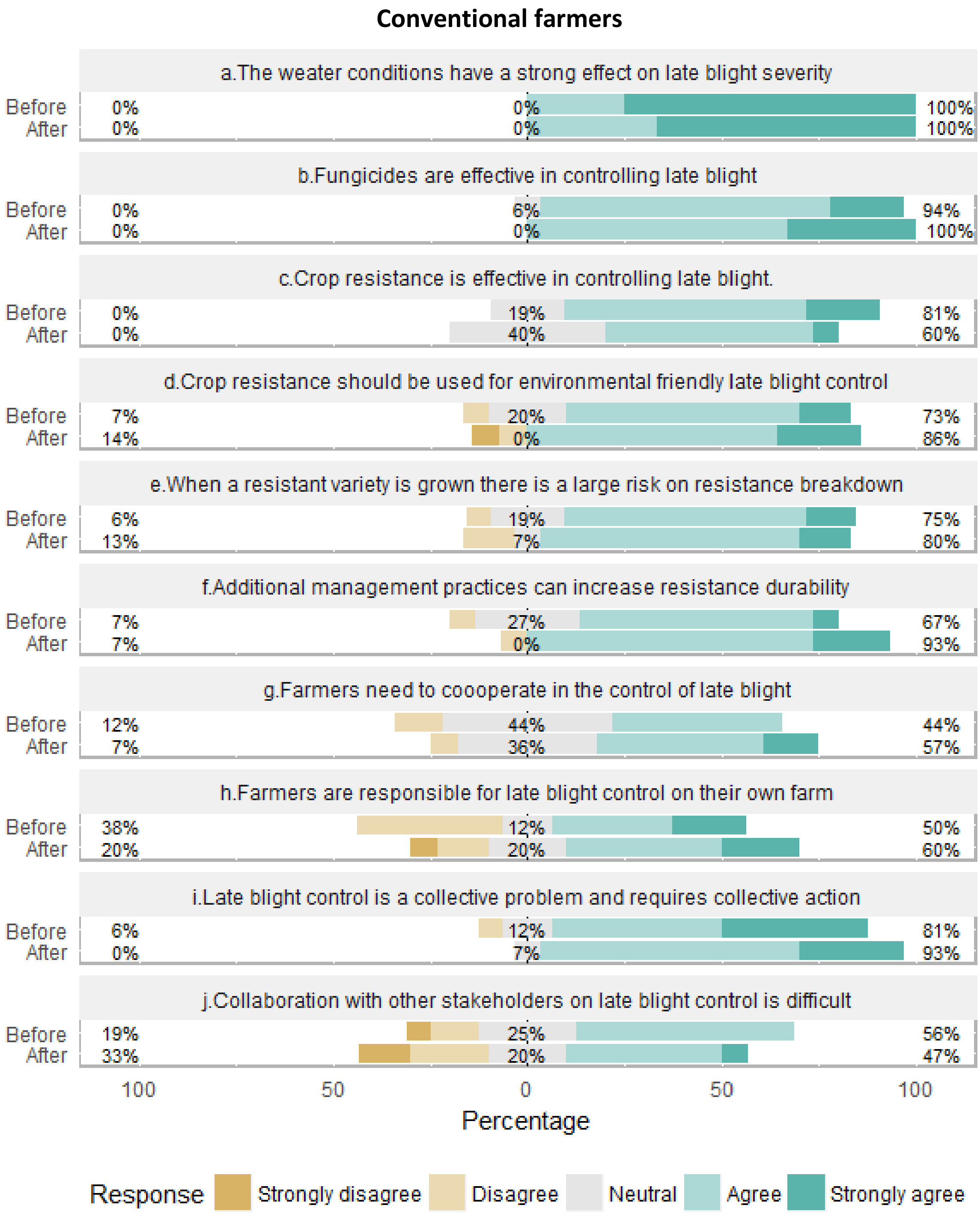

Figure 5.5. Statements on late blight control rated by farmers before and after the workshop using the Likert scale for conventional and organic farmers.

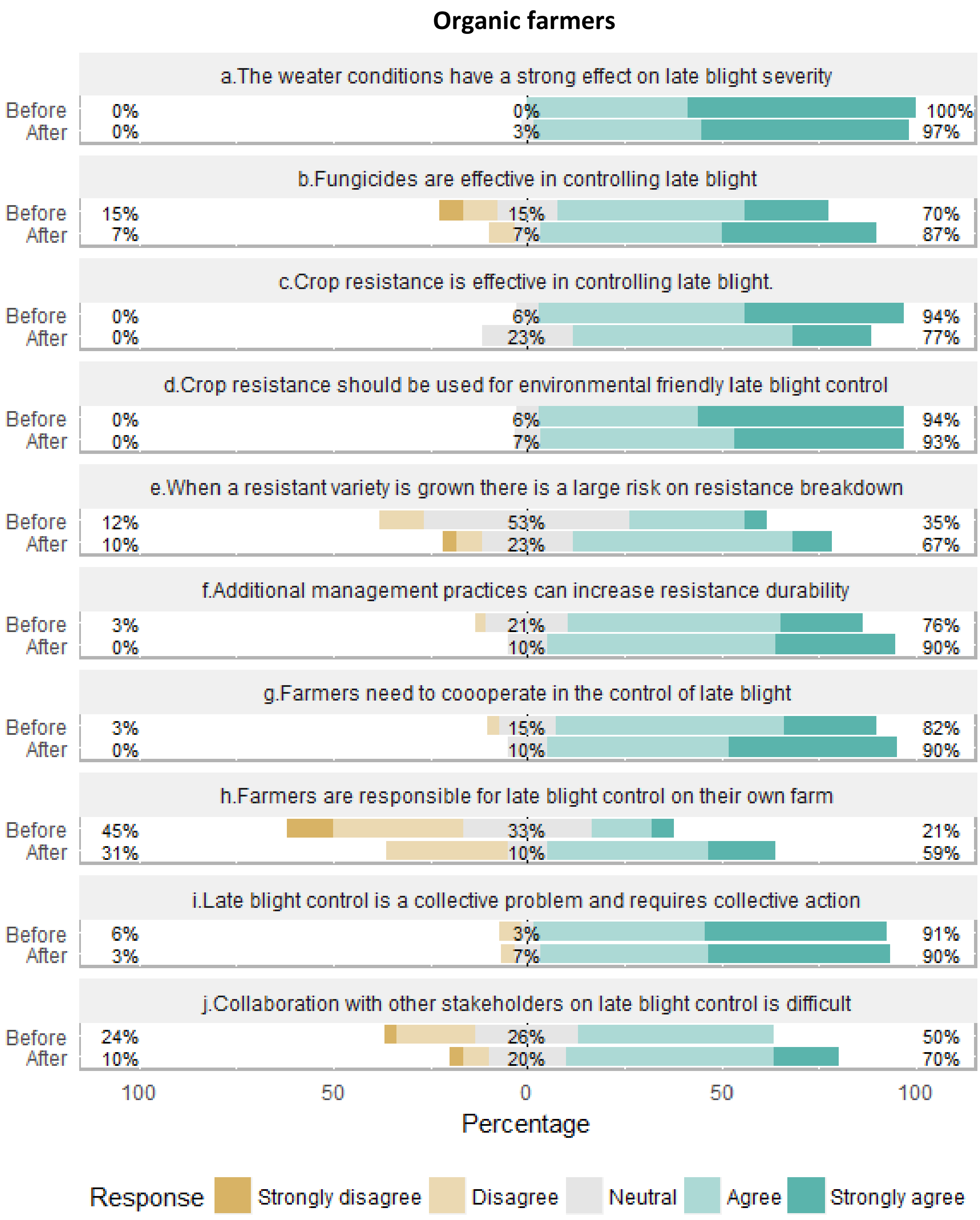

Figure 5.5. continued

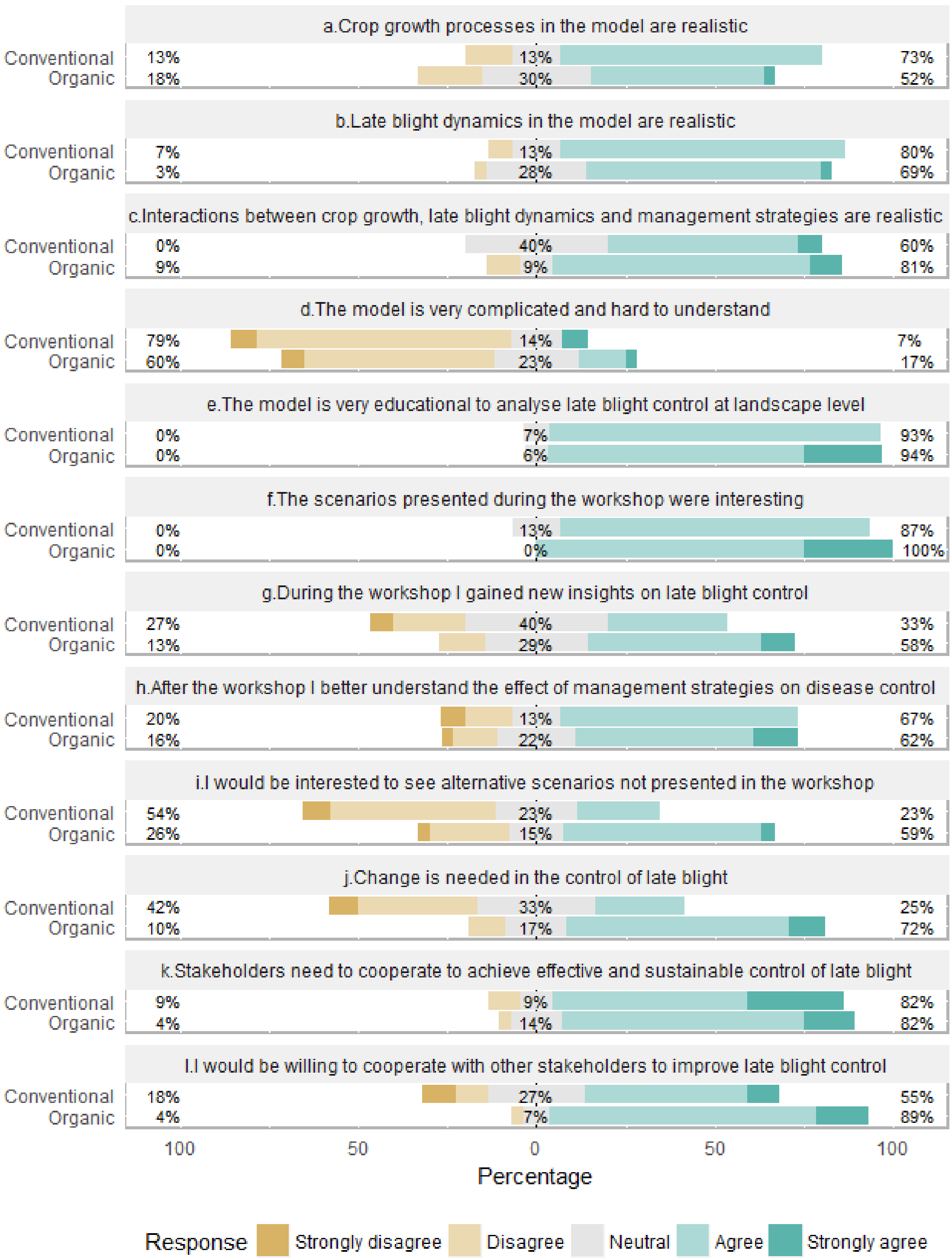

Figure 5.6. Results of the workshop evaluation form for conventional and organic farmers. Participants had to rate statements using the Likert scale.

After the workshop 72% of organic farmers thought that change is needed in the control of late blight (statement j) compared to 25% of conventional farmers (P=0.003). Most organic farmers agreed that they have to switch to resistant varieties: '*Breeding is very important. In agriculture chemicals have been used to control late blight* *for already 30 years and that is not the solution*' and '*We have to use resistant varieties with multiple resistance genes or destroy the haulm immediately after infection*'. Many conventional farmers did not believe change is needed or possible, supported by statements such as: '*For the moment we cannot do without fungicides*' and '*I think this is a great plea for developing resistant varieties and to continue spraying*'. Conventional farmers mentioned they want to use less fungicides but they feel it is not possible yet. They especially feel pressure from society since they feel people disapprove of their spraying practices.

A majority (82%) of both conventional and organic farmers agreed that stakeholders need to cooperate for effective and sustainable late blight control (statement k). For example one conventional farmer mentioned '*The importance of collective action is greater than expected*'. They believe the government, breeding companies and retailers/consumers play an important role in late blight control. Breeding companies are responsible for the development of new resistant varieties with multiple resistance genes. Secondly farmers thought that breeding companies should educate farmers how to cope with resistant varieties to prevent infections and increase resistance durability by providing support during cultivation. Both groups of farmers found that consumers and retail play an important role to increase the market share of resistant varieties. Some farmers also mentioned more regulation from the government is needed to support breeding programmes or monitor infections in resistant fields and emergence of virulent strains. Secondly, conventional farmers indicated that the government should change the regulations with respect to genetically modified crops so resistant varieties can be developed by inserting resistance genes in existing varieties using molecular techniques. In this way it is easier to develop resistant varieties with multiple resistance genes which also have all the other desired traits.

Farmers were also asked if they were willing to cooperate with other stakeholders on late blight control (statement l). Organic farmers were more willing to cooperate compared to conventional farmers (89% vs 55%, $P=0.044$). According to organic farmers cooperation is important to reduce the risk on resistance breakdown. One farmer stated that: '*Just a couple of farmers can ruin it for the others*'. However, they also felt it will be difficult to achieve this: '*There is no direct interest of farmers to destroy the haulm. There is a long-term interest but no short-term interest*'. In contrast, a conventional farmer mentioned the market mainly determines which varieties are produced which he cannot influence.

5.4 Discussion

Model findings

In this paper we report on workshops with farmers in which we used model-based scenarios to analyse the use of resistant varieties in disease control. The model showed that a large fraction of resistant fields can strongly reduce disease incidence in the landscape, however, after a couple of years resistance breakdown occurred by emergence of a new virulent *P. infestans* strain. If no countermeasures were taken the new virulent population could spread fast through the landscape, reducing potato yield of resistant fields. Furthermore, the model showed several resistance management strategies that could be effective to increase durability of resistant varieties.

Although no data was available on late blight dynamics at the landscape level over time to validate the model, the results can be supported by previous findings on late blight dynamics and other model studies. In the past it has been observed that resistance based on a single gene was overcome by *P. infestans* (Fry, 2008). It is argued that the risk of resistance breakdown is higher when there is a strong selection pressure. This occurs when a large area is planted with the resistant crop or exposed to a large *P.infestans* population (Haverkort et al., 2016). The use of fungicides in late blight control limits growth of the late blight population; the model showed that applying fungicides on all susceptible or all resistant fields was an effective way to increase resistance durability. Field experiments showed that infection in single-gene resistant potato varieties could be prevented by the application of fungicides using a reduced dose of 10-25% (Haverkort et al., 2016; Kessel et al., 2018). In the same study, infections in resistant varieties with multiple resistance genes were rare and some of these varieties remained healthy during two growing seasons. The chance that a virulent strain emerges that can overcome two resistance genes is very small since the responsible mechanisms are based on random events. In the scenario analysis the resistant variety with multiple resistance genes also did not get infected showing that gene stacking is an important strategy in resistance management.

The model showed that immediate haulm destruction after infections in resistant fields was effective in increasing resistance durability. In some of the years a small fraction of resistant fields was infected, but in the long term the resistance remained effective. During the growing season *P. infestans* strains are continually competing and the strain that can reproduce most rapidly can become dominant in the population (Cooke et al., 2012). Immediate haulm destruction could prevent spread of the virulent strain and establishment of the virulent strain in the population.

It was found that spatial allocation of resistant fields by clustering was not effective in preventing resistance breakdown. Once a resistant field was infected, the virulent strain could spread fast within a cluster of resistant fields. As a result, the virulent strain could establish in the population and the percentage of infected resistant fields increased. These results are in agreement with Skelsey et al. (2010) who found that clustering of potato fields in the landscape reduced spread between clusters but increased spread within a cluster, resulting in an overall net increase in disease incidence at landscape scale.

Effect of the workshop

To analyse the effect of the workshop, we assessed farmers' perceptions on late blight management before and after the workshop. Before the workshop many farmers were not aware that resistance breakdown could occur. The model provided more insight in this process and showed the emergence and spread of the virulent strain in an agricultural landscape over time. For conventional and organic farmers similar changes in perception were observed for almost all topics, showing that the workshop contributed to a common understanding on late blight control. After the workshop a large majority of the farmers agreed that stakeholders need to cooperate for effective and sustainable late blight control. By analysing the disease dynamics at the landscape level, the model showed the importance of collective action. Several resistance management strategies require farmer cooperation to keep disease pressure low and to prevent emergence and spread of the virulent strain (e.g. fungicide application, immediate haulm destruction). The majority of farmers was very positive about the workshop according to the evaluation survey conducted after the workshops. They stated that they found the model reliable, interesting scenarios were presented and their understanding of the effect of management strategies on disease control had improved (Figure 5.6). Although not all processes affecting crop and disease dynamics were included in the model, farmers were able to recognize the processes and patterns emerging from in the model. These results show that the scenario analysis increased farmers understanding of the system dynamics and the use of resistant varieties in late blight control.

During the workshop both short- and long-term strategies on late blight control were discussed by farmers, where long-term strategies included the development of resistant varieties with multiple resistance genes, and fungicide application and immediate haulm destruction as a short-term strategy. Secondly, farmers also discussed the boundaries of possible solutions. Several constraints were mentioned related to the institutional and political dimensions of crop protection. To achieve sustainable disease control farmers mentioned several stakeholders that play a role such as the government, breeding companies and retail. Changes in disease management require structural transformations and therefore it is important to use a system approach for the development of sustainable crop protection systems (Lewis et al., 1997; Schut et al., 2014). The use of model-based scenarios in workshops with farmers proved to be a very useful approach to discuss these aspects of late blight control. Therefore, it would also be interesting to organise these workshops with other groups of actors, such as breeding companies and policy makers.

Perceptions of conventional and organic farmers

Although the workshop contributed to a more shared understanding on late blight control some differences in perception were observed between conventional and organic farmers (Figures 5.5 and 5.6). These differences can be related to current farm practices and disease management strategies. For example, according to organic farmers resistance durability of single-gene varieties should be increased by immediate haulm destruction while conventional farmers preferred reduced use of fungicides. Overall, it was found that the workshop had a stronger effect on organic farmers. For example, conventional farmers showed no significant changes in perception before and after the workshop while organic farmers did (Figure 5.5). Secondly, organic farmers found the scenarios presented more interesting compared to conventional farmers and they were interested to explore more scenarios with alternative settings. Since the use of resistant varieties is an important method for disease control in organic farming the model results are much more relevant for this group of farmers. Organic farmers mentioned they would switch to resistant varieties and that additional resistance management practices are needed to increase resistance durability. Subsequently, the majority of organic farmers (72%) thought that change is needed in the control of late blight compared to 25% of conventional farmers. Since the use of fungicides (at reduced rates) can decrease the probability of infections in resistant fields, conventional farmers do not drastically have to change current practices.

To exchange views and to support collective decision-making processes it would be very interesting to organise joint workshop sessions with both types of farmers. With respect to late blight control a lot of tension exists between organic and conventional farmers which has resulted in conflicts in the past (Chapter 2). By collectively observing simulations stakeholders produce a shared understanding of the problem which can contribute to solve conflicts and negotiate possible (Barreteau, 2003). However, managing the diversity in stakeholders in participatory research can be challenging since differences in objectives and interests can lead to value-laden discussions which are often emotionally charged (Oteros-Rozas et al., 2015).

Improvements and further research

Using the model in workshops with farmers helped us to identify the strengths and weaknesses of the model. A strong point of the model is that late blight management strategies as well as infection with late blight were visualized in the model (Figure 5.1). During the simulation, the spread of the disease could be followed over time and space, which allowed workshop participants to relate the output variables to the agricultural landscape in the model. Agent-based models have a number of advantages compared to phenomenological models when communicating with non-scientist including dynamic visualisations and insight into states of individuals (Cartwright et al., 2016). These factors can help to communicate what the model is doing and increase understanding of the system by showing how patterns at system level emerge from individual behaviour.

Since no data was available on late blight dynamics at the landscape level over time to validate the model it should be used to generate general trends and patterns instead of making predictions for the future (Chapter 3). For researchers it is often challenging to explain to local stakeholders that the model is a simplified representation of reality rather than reality itself (Becu et al., 2008). Because of this, we believe the model can best be used in a guided workshop session. During the workshop we discussed uncertainties in model output and the feasibility of resistance management strategies. Cartwright et al. (2016) developed a framework for effective communication of complex ecological models and their outputs in which they also stress the importance of discussing uncertainties related to model results. Furthermore uncertainty in model output can help stakeholders to exchange views on knowledge and understanding of the system and in this way serve as a learning platform to integrate different views (Hedelin et al., 2017).

Although the model was very useful to show the effect of management strategies on disease control in an agricultural landscape, farmers mentioned some processes and management strategies which could be added to the model. One of the aspects that farmers missed in the model were processes on tuber blight. Infections in tubers can occur when spores produced on leaf and stem lesions are washed into the soil, resulting in yield losses in the field and during storage (Olanya et al., 2009). Besides the level and duration of foliar infections also many other factors have been reported that affect tuber blight including atmospheric conditions, soil factors, tuber resistance, management practices and cultivar architectural characteristics (Nyankanga et al., 2011; Nyankanga et al., 2007). Although it would make the model results with respect to potato yield more realistic for farmers, adding processes on tuber blight in a simplistic, yet realistic way will be challenging.

Secondly, for better involvement of conventional farmers the processes on fungicide application could be simulated in more detail, for example by implementing adaptive spraying regimes (instead of weekly application) and adding indicators related to fungicide costs and environmental pressure. The model scenarios shown in the workshop would probably be more interesting for conventional farmers when emphasising the potential benefits of resistant varieties related to reduced use of fungicides.

With respect to model scenarios organic farmers were interested to see landscape compositions with more diversity in resistant potato varieties (with different resistance genes). More diversity in crop resistance can potentially increase resistance durability and spread of virulent strains (Mundt, 2014), as has been found in a modelling study for yellow rust on wheat (Lof et al., 2017; Lof and Van der Werf, 2017). It would be interesting to implement these processes in the model and to present these scenarios in the workshop. Scenarios focusing on spatial allocation of resistant varieties would also be particularly interesting for breeding and trading companies since they are responsible for the development and distribution of potato varieties. Breeding for resistant varieties requires large investments so it is in their interest to protect these varieties from resistance breakdown. Organising workshops with these stakeholders would be interesting for further research.

5.5 Conclusion

In this research a previously developed agent-based model was used as a learning tool in workshops with groups of farmers (organic and conventional) to analyse whether resistant varieties can be used for sustainable control of potato late blight. During the workshop several scenarios were presented which showed disease dynamics at the landscape scale over ten years. The model showed the emergence of the virulent strain resulting in resistance breakdown and decreasing yield levels of resistant fields over time. Several resistance management strategies were presented which could be used to increase durability of resistant varieties. Our approach, in which we used model-based scenarios in combination with surveys and qualitative data was very useful to analyse farmers' perceptions on late blight control. The workshop contributed to a common understanding on late blight control and increased awareness that collective action is needed to achieve sustainable disease control. Secondly, the model scenarios were a good starting point for discussions among participants. In the workshop farmers exchanged views and negotiated possible solutions. Several other stakeholders were mentioned that play a role in disease management, such as breeding companies and policy makers. For further research, it would be valuable to organise similar workshops with these groups of actors.

Acknowledgements

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Chapter 6

General discussion

In the following sections the main findings of this thesis are summarised (Section 6.1), the methodology is evaluated (Section 6.2 and 6.3) and the implications for disease management are discussed (Section 6.4). Section 6.3 focuses on agent-based modelling which was an important tool in this study. Emergence of fungicide resistant *P. infestans* strains was not the main topic of this thesis but also very relevant in relation to this research and resistance management (Section 6.5). We discussed the relevance of the findings from this research for recent development in potato breeding (Section 6.6). Lastly, some ideas are discussed for future research on social-ecological systems and late blight control (Section 6.7).

6.1 Overview of the main findings

In this thesis we used a complex adaptive system approach to analyse the social-ecological system of potato late blight management. In Chapter 2 the fuzzy cognitive map provided an overview of the main concepts and relations in late blight control and showed that social and ecological processes are tightly linked. Three management scenarios were explored and it was found that increasing stakeholder cooperation and a change in market demands towards resistant cultivars could improve sustainability of late blight management. In contrast, policies restricting the use of fungicides would result in increased disease severity if no alternative strategies were implemented.

In Chapter 3 we showed how late blight severity, resistance durability and potato yield are affected by the spatial deployment of a single-gene resistant variety. Increasing the fraction of potato fields with the resistant variety strongly reduced late blight infection within a landscape. However, in the long term resistance breakdown occurred by emergence of a new virulent strain. The virulent strain gradually took over the pathogen population, decreasing mean potato yields from fields with the resistant variety. It was found that low as well as high proportions of fields with the resistant variety could increase durability of resistance. This finding can be explained with the dispersal scaling hypothesis (Skelsey et al., 2013). According to this theory, dispersal is maximized at intermediate scales as a result of interactions between dispersal distance and habitat size.

In Chapter 4 we analysed the interactions between farmers' behaviour and their interactions, potato crop performance and late blight control. The model reproduced a so-called boom-and-bust cycle. After introduction of a new resistant variety the percentage of farmers growing the resistant variety gradually increased (boom) until a virulent strain emerged. As a result of losses in yield and income in resistant fields farmers stopped growing the resistant variety (bust). A number of factors was identified that could affect resistance durability. The risk of emergence of the new virulent strain was positively affected by the fraction of susceptible fields without fungicides in the landscape. A higher crop price or yield of the resistant variety or higher fungicide costs increased the adoption of the resistant variety by farmers.

However, the majority of farmers continued growing the susceptible variety with fungicides, even if the resistance remained effective over longer periods. These results indicate that cooperation between actors in the whole sector is required to achieve structural transformations in disease control.

In Chapter 5 a modified version of the model from Chapter 3 was used as learning tool in workshops with conventional and organic farmers to show the effect of management strategies on disease dynamics at the landscape level. We explored several scenarios including a number of resistance management strategies. A number of resistance management strategies were identified that could potentially be effective to increase resistance durability including (reduced) use of fungicides on all resistant or all susceptible fields, growing a resistant variety with multiple resistance genes (instead of single-gene) and immediate haulm destruction of resistant fields after infection with the virulent strain. By showing disease dynamics at the landscape scale the model increased awareness that collective action is needed to achieve sustainable disease control. Analysing model-based scenarios in workshops was very useful for increasing farmers' knowledge of the system and served as a good starting point for discussions among actors. Furthermore, the workshop was a useful means to analyse farmer perception on late blight control and differences in response were found between organic and conventional farmers.

6.2 Methodology

In this thesis a collection of methods was used to analyse sustainable management strategies in potato late blight including in-depth interviews, fuzzy cognitive mapping, agent-based modelling, scenario analysis and participatory modelling. Each of these methods was used to analyse different aspects of the complex social-ecological system. Semi-structured interviews with actors (farmers, breeding companies and experts) were used to develop a broad perspective on the issues in potato production and late blight management as well as differences in management strategies of farmers. Furthermore, the interviews increased insight in stakeholder objectives and the factors involved in decision making. This information was also used to develop and validate the framework on farmer behaviour in the agent-based model.

Fuzzy cognitive mapping was a useful tool in summarising the most important components and relations influencing late blight severity and management. This technique allows to integrate social and ecological factors. The model highlights the interactions and feedback loops in the system. We analysed several scenarios and identified strategies and drivers that could positively affect sustainable disease control. In the fuzzy cognitive map, relations between components represent positive or negative influences. A limitation of this method is that not all types of interaction can be mapped, for instance social interactions between (groups of) stakeholders. Secondly, a fuzzy cognitive map cannot represent non-linear relations, discrete events and tipping points such as resistance breakdown by emergence of virulent strains. Fuzzy cognitive mapping is a semi-qualitative tool: the model steps do not represent a certain time scale since the processes act on different scales and the model output variables are relative since they do not represent certain units. Therefore, methods such as agent-based modelling could be more appropriate for analysing the system dynamics when the processes and interactions of the different components are more or less understood.

In this thesis agent-based modelling was used for (i) analysing crop-disease interactions affected by management strategies at the landscape level, (ii) analysing social-ecological interactions between farmer behaviour and disease dynamics and (iii) communicating the dynamics in the complex system to stakeholders. The epidemiological framework was based on existing models and data on late blight dynamics. The framework on farmers' decision making was based on a behavioural theory and supported by data from literature and interviews with Dutch potato farmers. The models can be described as so-called mid-range models: the purpose is not to exactly model the situation in a certain region, nor to make a purely theoretical point (Gilbert, 2008). Since no specific data in time and space was available on late blight dynamics and farmer behaviour to validate the results the models should be used for obtaining an understanding of the system behaviour rather than for making predictions. The trends and patterns emerging from the model could be supported by previous findings on late blight dynamics and farmer behaviour. The model increased understanding on the use of crop resistance in disease control. Several factors were identified that influenced resistance durability and the adoption of resistant varieties by farmers. The agent-based model also proved useful in the analysis of how actions by stakeholders could affect farmer behaviour and late blight control.

The model was used in workshops with conventional and organic farmers to demonstrate and discuss the potential role of resistant varieties for effective and sustainable control of late blight. During the workshop questionnaires and surveys were used to analyse farmer perception on disease control. In participatory modelling these methods have been recognized as appropriate tools for evaluating the learning process (Mayer et al., 2014; Voinov and Bousquet, 2010). Clear differences were found between conventional and organic farmers. According to a conventional farmer the model results were 'a great plea to continue spraying and to develop resistant varieties' while organic farmers stressed the importance of resistance management strategies by immediate haulm destruction. So although the same scenarios were presented, the model results are interpreted in a different way. According to Ditzler et al. (2018) it is important to focus on the interactions between the tool and the user to evaluate the use of a tool in participatory settings. Especially when the tool is used to support participatory problem-solving it is important to analyse how different stakeholders interact with the model.

In this study model-based scenarios were presented to a group of actors, but agent-based models are also very suitable to use in a more interactive and participatory way (Bousquet and Le Page, 2004; Ramanath and Gilbert, 2004). In participatory settings stakeholders can select and explore scenarios themselves and for this purpose users are often involved in an early stage of model design to identify scenarios of interest (Dolinska, 2017). This also relates to 'companion modelling' which is a cyclic approach based on repetitive back and forth steps between the model and the field situation (Barreteau, 2003). The approach can serve different purposes: learning about the system behaviour or support collective decision processes.

Fuzzy cognitive mapping and agent-based modelling were complemented with scenario analysis in workshops as an effective method in participatory research to show the effect of current management strategies and to discuss opportunities for change, and the application of surveys and questionnaires to analyse the perception of individual people or groups. The combined and complementary use of a collection of methods contributed to increased understanding of the system components and their interactions. Such a portfolio approach is recommended to analyse problems in social and ecological systems. These problems often emerge due to scale mismatches in processes in space and time and the occurrence of unanticipated events and interactions (Cumming et al., 2006; Satake et al., 2008). Spatial scale mismatches concern small versus large scale processes, such as leaf infection and spore dispersal in the biophysical domain, and farmer decision-making for field management versus system innovation at (supra-) national level in the socio-institutional domain. In our case study we encountered interacting processes at different temporal scales (fast and slow), for instance the fast process of pathogen adaptation and the slow process of breeding a new variety, and moreover the contrasting time scales of the fast switching from preventive to curative fungicides and the slow emergence of negative effects of fungicides on environmental and human health. As a consequence, the system dynamics are difficult to capture and outcomes of system analysis and development options are often debated, as demonstrated by the diverging perceptions of organic and conventional farmers in this thesis. Use of different methods allows the development of a more comprehensive and multidimensional perspective on the problem, opens broad opportunities for discussion, and can inform collaborative decision making and policy development.

6.3 Agent-based modelling

Although agent-based models are very suitable to analyse social-ecological systems due to their flexibility in temporal and spatial scales and the scheduling of dynamics, the number of models that couple two-way feedbacks between human and natural systems is limited (Filatova et al., 2013). The strength of agent-based models to analyse complexity also relates to its main challenge. Because biophysical and socio-economic models often work at different scales integration can be difficult and decisions need to be made how the systems can be linked in terms of interactions and feedback mechanisms (Parker et al., 2008). Furthermore these models can include many parameters which means they can be very data demanding. Potato late blight presented a unique case study since this topic has been widely investigated and much data is available on *P. infestans* epidemiology and its management. However, coupling the social and ecological system required strong simplifications of both host-pathogen interactions and the decision-making of agents and their interactions. The agent-based models from this thesis showed how management decisions and disease dynamics can be integrated. Details on management strategies, crop and disease processes and climate and landscape data need to be adapted to the specific case study but the general model structure could be useful in model development. Relevant model elements include the interactions and feedback mechanisms between farmer behaviour, management strategies and disease dynamics, the integration with climate and landscape data, representation of social-economic drivers, and the use of a behavioural theory to simulate farmer behaviour.

An additional challenge lies in the validation of these models (Gilbert, 2004; Schulze et al., 2017; Troitzsch, 2004). The models often represent dynamics on large temporal and spatial scales and in most cases it is impossible or too expensive to collect this type of large scale data; related to host-pathogen dynamics as well as human behaviour for individuals or groups. Other methods such as expert validation or pattern-oriented modelling might therefore be more appropriate (Grimm et al., 2005; Schulze et al., 2017). It has also been proposed that the required level of validation is dependent on the purpose of the model which is usually more focussed on understanding instead of predicting (Verburg et al., 2016). As a result of these challenges, fuzzy cognitive mapping could serve as starting point in the analysis of social-ecological systems to get an overview of the system components and their interactions, to make decisions on the system boundaries and to identify potential knowledge gaps.

6.4 Implications for disease management

In this thesis potato late blight was analysed as a social-ecological system to identify factors that could contribute to the development of sustainable disease management strategies. In the Netherlands about 50% of the total volume of fungicides is used in late blight control so there is strong need for alternative, more sustainable strategies. We conclude that resistant varieties could contribute to sustainable disease control when combined with resistance management. The results showed that there is a large risk that new virulent strains emerge that can overcome resistance of single-gene resistant varieties. This risk increases with larger fractions of resistant varieties in the landscape with the same resistance gene. Recently, the organic sector agreed to upscale the use of resistant varieties and that all organic farmers will switch to resistant varieties the coming years (Bionext, 2017). Although organic potato production is only covering 1% of the total potato production, farmers and breeding companies must be made aware of the increasing risk of resistance breakdown. Especially in the transition period, where organic farmers grow a mix of susceptible and resistant varieties, there is a high risk of infection since virulent spores emerging from susceptible fields can easily spread to neighbouring resistant fields.

For breeding companies and farmers this is relevant information that stresses the importance of resistance management strategies. The model showed that resistant varieties with multiple resistance genes could increase resistance durability. However, when these varieties contain resistance genes that have also been used in single-gene varieties, these can serve as a stepping stones for the pathogen to overcome resistance of multiple-gene resistant varieties (Lof et al., 2017). Breeding companies could use this information to make decisions on breeding and marketing strategies.

A number of strategies were identified that could increase durability of single-gene resistant varieties including (reduced) use of fungicides on all resistant or all susceptible fields and immediate haulm destruction of resistant fields after infection with the virulent strain. In the workshop with farmers it was found that immediate haulm destruction after infections in resistant fields could be an effective strategy for organic farmers by preventing spread of the virulent strain. To manage resistance, conventional farmers preferred reduced use of fungicides on resistant fields which provides additional protection.

With respect to resistance management it is important that all farmers cooperate to keep disease pressure low to prevent emergence and spread of virulent strains. The model analysis showed that resistance breakdown is a highly unpredictable process and results from interactions between the weather conditions and the allocation of potato varieties. Therefore farmers must pay attention at all times and must regularly inspect their potato fields. Secondly, to increase the use of crop resistance in disease control cooperation between stakeholders in the whole production chain is required, which can be demonstrated with the Dutch organic potato sector. Stakeholders including farmers organisations, breeding companies and supermarkets recently agreed to switch to 100% resistant varieties the coming years (Bionext, 2017). Late blight epidemics since 2000 have caused major losses in yield in organic potato production and a severe epidemic in 2016 was the last push leading to this agreement. According to Nuijten et al. (2017) a pull factor is required for successful market introduction of disease resistant crops and there must be an urgent need among stakeholders for successful cooperation. Based on the results from the interviews and workshops it can be concluded that conventional farmers did not feel an urgent need for change. It is therefore also not expected that a similar transition in the conventional sector will soon follow. A pull factor leading to change could for example be the emergence of fungicide resistant strains (see Section 6.5).

6.5 Fungicide resistance

Fungicide insensitivity as described in Chapter 2 was not a topic further investigated in this thesis where we focussed on the use of resistant varieties and resistance durability. However, in the same way as new virulent strains emerge that are able to overcome resistance in the host also new strains can emerge which become insensitive to fungicides. A fungicide called metalaxyl used to be effective in late blight control, however, the performance rapidly decreased by emergence of metalaxyl-resistant strains in many countries including the Netherlands (Gisi and Cohen, 1996). A fungicide containing this compound was registered in 1979 but already one year later a late blight outbreak caused by a metalaxyl-resistant *P. infestans* population resulted in considerable financial losses for many farmers (Davidse et al., 1981). At that moment the specific fungicide was already applied to 50% of the total potato acreage. Experiments showed that metalaxyl-resistance was a monogenic trait, so governed by a single gene (Shattock, 1988). Emergence of metalaxyl-resistant strains therefore requires only one or at most a few mutations. In the gene-for-gene model the interaction between plant resistance and virulent pathogens is also based on single genes (Flor, 1971). The processes related to resistance breakdown of a single-gene variety and fungicide insensitivity of a single-site-acting fungicides could therefore act in a similar way.

To prevent fungicide insensitivity a number of resistance management strategies have been proposed including (i) dose reduction, (ii) fungicide mixtures, (iii) alternation of fungicides, and (iv) spatial and temporal diversity in the use of fungicides (Brent and Hollomon, 1995). These strategies are very similar to the proposed resistance management strategies related to crop resistance. In that case the word 'fungicide' can be replaced by 'resistance gene' (Mundt, 2014). The effectiveness of these strategies have been analysed by experiments and modelling studies (Brent and Hollomon, 1995; Hobbelen et al., 2013; Van den Bosch and Gilligan, 2008). In general, the use of fungicide mixtures and fungicide alternation have been recognized as effective strategies to manage fungicide resistance (Van den Bosch and Gilligan, 2008). The implementation of these strategies can be challenging since it requires cooperation between manufacturers and farmers (Brent and Hollomon, 1995). Nevertheless, soon after the first metalaxyl-resistant strains emerged in 1980 the agrochemical industry agreed to cooperate and set up a group called Fungicide Resistance Action Committee (FRAC). The purpose of this group is to investigate resistance problems and to establish countermeasures. The FRAC has played a major role in developing and implementing resistance management strategies.

To develop and implement resistance management strategies it is interesting to study and learn from both cases. The use of fungicides is more flexible in time and involves less stakeholders compared to the use of crop resistance. Because variety choice is largely influenced by the market demands, and since potatoes are reproduced vegetatively and the reproduction factor is low, it is not possible to switch to other varieties from one year to the other for a large group of farmers. The development and implementation of resistance management strategies related to spatial and temporal allocation of resistant varieties is therefore challenging. However, developments in potato breeding could offer new opportunities (see Section 6.6). To increase resistance durability and prevent fungicide insensitivity it has also been suggested to combine crop resistance with reduced use of fungicides. In general, based on the findings of this thesis and the case of fungicide resistance it can be concluded that cooperation between stakeholders is required for effective implementation of resistance management strategies.

6.6 Developments in potato breeding

Over the last years research on potato and late blight has progressed and some new breakthroughs have been achieved in the development of resistant varieties. To mitigate the risk of resistance breakdown as a result of pathogen adaptation, researchers and breeding companies continued to develop varieties with more durable resistance. The program Bioimpuls aims at developing varieties with multiple resistance genes using classical breeding with more than ten different resistance sources (Lammerts van Bueren et al., 2008). Breeding for resistance is a time-consuming process and takes large investments. It can take multiple decades to introgress a single resistance gene from wild relatives. The use of molecular markers to identify resistance genes (marker assisted selection) is an important method to improve and speed up the crossing and selection process when combining various resistance genes (Schaart et al., 2016). As the results from our project, as well as many other studies show, stacked resistance is an important strategy to increase resistance durability. Despite the long process varieties with multiple resistance genes are already expected to enter the market the coming years. Recently the organic sector made an agreement to switch to 100% resistant varieties in 2020 (Bionext, 2017). Currently, ten resistant potato varieties are available on the market and their resistance is based on five different resistance sources (personal communication, R. Hutten 2017). More diversity in varieties with different resistance genes could potentially reduce the emergence and spread of virulent strains (Lof et al., 2017; Mundt, 2014).

Besides the development of resistant varieties through classical breeding also molecular techniques have been used to develop resistant varieties. In the project DuRPh, resistance genes have been introgressed into existing varieties by a technique called cisgenesis (Haverkort et al., 2016). This process is much faster compared to classical breeding and the varieties already have the specific traits required by the market. However, this technique does not seem to work with all existing varieties and also the long-term effect of these insertions is unknown. Due to European regulations on GMO crops the growth and production of these cisgenic potatoes is strictly regulated. Cisgenesis does also not comply with the norms and standards of organic agriculture so cisgenic resistant potato varieties are not an option for this sector (Lammerts van Bueren et al., 2008). On the other side, the results from interviews and workshops showed that conventional farmers are positive about growing these varieties. So in case the regulations will change these varieties could potentially contribute to sustainable disease control by reducing the amount of fungicides. However, whether cisgenic potatoes could play a significant role in sustainable disease control is dependent on a large group of stakeholders since retailers and consumers also play an important role in the selection and acceptance of potato varieties.

The last years a number of researchers and breeding companies have been working on the method of F1 hybrid potato breeding which can be used to develop resistant potato varieties (Lindhout et al., 2011). In this method homozygous parental lines are developed and by crossing these lines hybrid offspring is created which are genetically identical. The use of homozygous parental lines speeds up the breeding process since it is easier to combine specific potato traits in one variety by crossing. An additional effect is that potatoes do no longer have to be reproduced vegetatively by the production of seed potatoes but can be grown from seeds, which can cause a revolutionary change in potato production. As a result of fast reproduction it could be easier to introduce new varieties and also the export of seeds compared to seed potatoes has benefits. A Dutch company is using this method to develop late blight resistant potato varieties with multiple resistance genes and they aim to introduce the first hybrid resistant variety in the next five years.

As a result of these advancements in potato breeding it is expected that more resistant varieties will enter the market the coming years and their acreage will increase. The findings from this study related to resistance durability and resistance management are very relevant in this context, especially since upscaling the use of resistant potato varieties can increase the risk that new virulent strains emerge and spread. Also new breeding techniques affect both social and ecological systems which stresses the importance of an interdisciplinary approach to analyse how these developments can contribute to sustainable disease control.

6.7 Future research

The methods used in this thesis increased understanding of the social-ecological system of potato late blight. A number of factors and processes were identified that could contribute to the development of sustainable late blight management strategies. For further research on potato late blight it would be interesting to explore some of the processes and interactions related to disease control in more detail using agent-based modelling. For example, scenarios could be modelled that analyse the effect of spatial and temporal allocation strategies of potato varieties with different resistance genes on resistance durability. Secondly, interactions between farmers and other groups of actors and institutions could be implemented to analyse the socio-institutional interactions related to disease control. It would be interesting to organise workshops with other groups of actors such as breeding companies and policy makers to inform discussions and negotiations among stakeholders and to support learning and decision-making.

Analysing the social-ecological interactions on potato late blight control proved very useful for increasing understanding of the system behaviour which is necessary for developing effective strategies. Therefore the methods used in this thesis might be very relevant for a range of case studies focusing on management of crop-disease interactions. Emerging infectious diseases of crop plants are one of the main threats in agriculture which can have large social, economic and environmental consequences (Vurro et al., 2010). Furthermore as a result of globalization, increasing human mobility, climate change, and evolution and adaptation of pathogens or their vectors the risk of invasions of plant pathogen increases (Anderson et al., 2004). For example, at the beginning of the 21st century Banana Xanthomonas wilt (BXW) rapidly spread all over Africa causing drastic reductions in banana production with resulting economic and social problems.

Disease control in agriculture is the result of social and biophysical processes and their interactions. We showed a number of methods that could be used to analyse the social and ecological processes and their interactions. These methods focussed on different aspects of the system and the results from this thesis showed that they are complementary to each other in terms of the ability to represent complex dynamics such as social-ecological interactions, non-linear relations and tipping points, integration between system components, and focus on social/biophysical components. For future research on social-ecological systems a portfolio approach, that involves a collection of complementary methods, could contribute to the analysis of these systems and the development of policies.

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Summary

The world of today is facing many challenges such as environmental pollution, coping with climate change and producing food for an increasing human population. To find solutions for these problems one has to deal with human and natural systems. These systems can be described as *complex* and *adaptive*. *Complex* means that they consists of many different components that interact across multiple temporal and spatial scales. Secondly, these components also *adapt* to each other and their environment. Within a Complex Adaptive Systems (CAS), patterns at system level emerge from interactions between individual components. By focusing on the interactions between system components, a CAS-approach (considering the system under study as a CAS) can increase understanding of the mechanisms underlying system behaviour which can contribute to the design of effective management strategies. Social-ecological systems (SES) are a case of CAS which specifically focus on the interactions and feedback mechanisms between humans and the environment. In this thesis potato late blight is analysed as a model system for studying social-ecological processes and for finding options for improved management and governance of crop-disease interactions in landscapes.

Potato late blight (caused by *Phytophthora infestans*) is one of the main diseases in potato production. Infection with late blight results in foliage death and tuber rot in the field and in storage. In case of favourable weather (moderate temperatures and high humidity) the pathogen can spread in a short time over large distances due to its short life cycle, the high spore production and spore dispersal by wind. Furthermore the pathogen can adapt rapidly to its host and the environment due to the high plasticity in the genome. In this thesis we focus on the Netherlands which is a large producer of seed, ware and starch potatoes. Late blight is a serious problem because of the high potato density and favourable weather conditions for the disease. In conventional agriculture fungicides are applied but these are harmful for the environment. It is estimated that about 50% of all fungicides applied in the Netherlands is used in late blight control. Since chemicals are not allowed in organic agriculture potato yields can be dramatically low in years with severe outbreaks of the disease. In contrast to some other European countries, also fungicides based on copper are not permitted in the Netherlands. To reduce the amount of fungicides in conventional systems and to improve disease control for organic farmers the development of late blight resistant varieties is a top priority. New late blight resistant varieties have been entering the Dutch market since 2007, and have so far mainly been used in organic farming systems. The resistance is the result of resistance genes and non-compatible pathogens are unable to infect the host. However, due to pathogen adaption new virulent strains can emerge which can overcome resistance. Furthermore

this new generation of late blight resistant varieties has moderate yield levels and does not meet all market requirements compared to those of regular (susceptible) varieties.

Overall, spread of the disease is affected by biophysical processes related to crops and pathogens as well as decision-making processes on crop management. The general objective of this thesis is to analyse potato late blight control as a social-ecological system to increase understanding of the system behaviour and to identify factors and processes that could contribute to the development of sustainable disease management strategies. A collection of methods was used for increasing understanding of the components and interactions within the social-ecological system.

In Chapter 2 we present an overview of the social-ecological system of potato late blight. To analyse and describe the components, the interactions and feedback mechanisms related to late blight management, three different methods were used; 1) literature search on late blight management, 2) semi-structured interviews with stakeholders and 3) a modelling exercise called fuzzy cognitive mapping. The results show that published research on late blight mainly focuses on agronomic practices, plant breeding for resistance to late blight and chemical-based disease suppression. In-depth interviews were carried out with farmers, representatives of breeding companies and experts. The results show that many different stakeholders are involved in late blight control and each of them have their own objectives and interest. This leads to various types of interactions such as competition, cooperation and trading. Farmers play a key in the system since they make decisions on crop management but they are strongly influenced by traders, breeders, public institutes and policies. The fuzzy cognitive map summarised the most important concepts and relationships related to late blight control. The fuzzy cognitive map showed that social and ecological processes are tightly linked and several feedback loops were identified. The fuzzy cognitive map was used to explore several management scenarios. It was found that that increasing stakeholder cooperation and a change in market demands towards resistant varieties could improve sustainability of late blight management. In contrast, policies restricting the use of fungicides would result in increased disease severity if no alternative strategies were implemented. Adoption of such strategies would require social-institutional support and facilitation.

In Chapter 3 a spatially explicit agent-based model was developed to analyse the use of crop resistance in disease control. The model simulates crop-disease interactions in an agricultural landscape affected by the weather conditions and management strategies of farmers. The epidemiological framework was based on existing models and data on late blight dynamics. The model was applied to an agricultural region in the Netherlands (the Noordoostpolder; 596 km^2) and was run for a period of 36 years using daily weather data as input for crop growth and disease dynamics. The model was used to analyse how late blight severity, resistance durability and potato yield are affected by the spatial deployment of a (single gene) resistant variety. The results showed that increasing the fraction of potato fields with the resistant variety strongly reduced late blight infection within a landscape. However, in the long term resistance breakdown occurred by emergence of a new virulent strain. The virulent strain gradually took over the pathogen population, decreasing mean potato yields from fields with the resistant variety. It was found that low as well as high proportions of fields with the resistant variety could increase durability of resistance. This pattern can be explained with the dispersal scaling hypothesis. According to this theory, dispersal is maximized at intermediate scales as a result of interactions between dispersal distance and habitat size.

In Chapter 4 we extended the agent-based model of Chapter 3 by adding the dimension of farmers' decision making. The agent-based model was used to analyse the interactions between farmer behaviour and late blight dynamics. The framework on farmers' decision-making was based on a behavioural theory and supported by data from literature and interviews with Dutch potato farmers. We assumed a scenario where a new (single gene) resistant variety was introduced to the market. The model was used to analyse the adoption of a late blight resistant variety by farmers and the durability of resistance over time. The model reproduced a so-called boom-and-bust cycle: the percentage of farmers growing the resistant variety increased (boom) until resistance breakdown occurred by emergence and spread of a virulent strain, and in response farmers switched to other potato varieties and management strategies (bust). Resistance breakdown did not occur in all model runs and was the result of interactions between management strategies of farmers, the weather conditions and the allocation of potato varieties in the landscape. Higher fungicide costs and higher yield or crop price of the resistant variety increased the adoption of the resistant variety. However, also a large number of farmers continued growing the susceptible variety with fungicides which suggests that cooperation in the whole potato sector is needed to achieve structural transformations in disease control. In addition, the risk on resistance breakdown stresses the importance of resistance management strategies to increase resistance durability.

In Chapter 5, a modified version of the agent-based model of Chapter 2 was used in workshops with conventional and organic farmers. The model was used as a learning tool to increase farmers' understanding of the system dynamics and to demonstrate and discuss the potential role of resistant varieties for effective and sustainable control of late blight. Several model-based scenarios were presented related to the use of crop resistance and fungicide application on disease control at the landscape level. Qualitative and quantitative measures were used to analyse the effect of the workshop on farmers' perception on late blight control. The model showed a number of resistance management strategies that could be effective to increase resistance durability including (reduced) use of fungicides (in conventional production systems) on all susceptible or all resistant fields, growing a resistant variety with multiple resistance genes (instead of single-gene) and immediate haulm destruction of resistant fields after infection with the virulent strain. The workshop was very useful to

analyse changes in farmer perceptions. Before the workshop many farmers were not aware that resistance breakdown could occur. After the workshop a large majority of the farmers agreed that stakeholders need to cooperate for effective and sustainable late blight control. By analysing the disease dynamics at the landscape level, the model showed the importance of collective action. For conventional and organic farmers similar changes in perception were observed for almost all topics, showing that the workshop contributed to a common understanding on late blight control.

In Chapter 6 we discussed the main findings of this thesis and evaluated the methodology. A number of factors and processes were identified that could contribute to the development of sustainable late blight management strategies. We conclude that resistant varieties can contribute to sustainable disease control but resistance management strategies are required to increase resistance durability. To achieve this cooperation between stakeholders in the whole potato sector is required. Furthermore to prevent emergence and spread of virulent strains it is important that all farmers cooperate to keep disease pressure low. Recently, stakeholders in the organic sector agreed to switch to 100% resistant varieties the coming years. Furthermore as a result of developments in potato breeding it is expected that new late blight resistant varieties will enter the market the coming years. As a result of these changes it is expected that the acreage of resistant varieties will increase in the future. The findings from this study related to resistance durability and resistance management are very relevant in this context, especially since upscaling the use of resistant potato varieties can increase the risk that new virulent strains emerge and spread. Also new developments affect both social and ecological systems which stresses the importance of an interdisciplinary approach. To analyse the social-ecological system of potato late blight a collection of methods was used including in-depth interviews, fuzzy cognitive mapping, agent-based modelling, scenario analysis and participatory modelling. The combined and complementary use of these methods contributed to increased understanding of the system components and their interactions. For future research on social-ecological systems such a portfolio approach could contribute to the analysis of these systems and the development of policies.

Samenvatting

De wereld van nu staat voor vele uitdagingen zoals milieuvervuiling, de aanpak van klimaatverandering en het produceren van voedsel voor de groeiende bevolking. Om oplossingen voor deze problemen te vinden, heeft men te maken met menselijke en natuurlijke systemen. Deze systemen kunnen worden omschreven als *complex* en *adaptief*. *Complex* betekent dat ze uit veel verschillende componenten bestaan die interacteren op meerdere temporele en ruimtelijke schalen. Adaptief betekent dat deze componenten zich aan elkaar, en aan hun omgeving aanpassen. In een Complex Adaptief Systeem (CAS) ontstaan patronen op systeemniveau uit interacties tussen de afzonderlijke componenten. Door te focussen op de interacties tussen systeemcomponenten, kan een CAS-benadering (het systeem bestuderen als een CAS) het begrip vergroten van de mechanismen die ten grondslag liggen aan systeemgedrag. Dit kan bijdragen aan het ontwikkelen van effectieve strategieën. Sociaal-ecologische systemen (SES) zijn een soort CAS, maar hierbij ligt de focus specifiek op de interacties tussen mens en milieu. In dit proefschrift wordt de aardappelziekte geanalyseerd als een modelsysteem voor het bestuderen van sociaal-ecologische processen en voor het vinden van strategieën om gewas-ziekte interacties in landschappen te beheren.

De aardappelziekte of phytophthora (veroorzaakt door *Phytophthora infestans*) is een van de belangrijkste ziektes in de aardappelteelt. Infectie met phytophthora veroorzaakt afsterving van de bladeren, en knolrot in het veld en in de opslag. Vanwege de korte levenscyclus, het produceren van grote aantallen sporen en sporenverspreiding door de wind kan de ziekte zich bij gunstig weer (gematigde temperaturen en hoge luchtvochtigheid) snel verspreiden over grote afstanden. Bovendien kan het pathogeen zich vanwege het dynamische genoom snel aanpassen aan zijn omgeving. In dit proefschrift richten we ons op Nederland, een grote producent van pootaardappelen, consumptieaardappelen en zetmeelaardappelen. Phytophthora is een ernstig probleem vanwege de hoge aardappeldichtheid en gunstig weer voor verspreiding van de ziekte. In de gangbare landbouw worden fungiciden gebruikt, maar deze zijn schadelijk voor het milieu. Geschat wordt dat ongeveer 50% van de totale hoeveelheid fungiciden in Nederland wordt gebruikt voor de beheersing van phytophthora. Aangezien chemische middelen niet zijn toegestaan in de biologische landbouw, kunnen de aardappelopbrengsten erg laag zijn in jaren met een hoge ziektedruk. In tegenstelling tot sommige andere Europese landen zijn in Nederland ook fungiciden op basis van koper niet toegestaan. Om de hoeveelheid fungiciden in de gangbare landbouw te verminderen en de ziektebeheersing voor biologische telers te verbeteren, is de ontwikkeling van aardappelrassen die resistent zijn tegen phytophthora een hoofdprioriteit. Nieuwe phytophthora-resistente rassen zijn sinds 2007 op de Nederlandse markt en worden tot nu toe vooral gebruikt in de biologische teelt. Deze rassen bevatten resistentiegenen waardoor de plant niet geïnfecteerd kan worden. Door aanpassing van het pathogeen kunnen echter nieuwe virulente stammen ontstaan die de resistentie kunnen doorbreken. Bovendien heeft deze nieuwe generatie resistente rassen een matige opbrengst en voldoet ze niet aan alle markteisen in vergelijking met reguliere vatbare rassen.

Verspreiding van de ziekte wordt beïnvloed door biofysische processen met betrekking tot het gewas en de ziekteverwekker en door besluitvormingsprocessen over gewasbeheer. De algemene doelstelling van dit proefschrift is om de beheersing van phytophthora te analyseren als een sociaal-ecologisch systeem om inzicht te krijgen in het systeemgedrag en om factoren en processen te identificeren die kunnen bijdragen aan de ontwikkeling van duurzame beheersingsstrategieën. Een aantal verschillende methoden werden gebruikt om de componenten en interacties binnen het sociaal-ecologische systeem in kaart te brengen en te analyseren.

In Hoofdstuk 2 geven we een overzicht van het sociaal-ecologische systeem van de aardappelziekte. Drie verschillende methodes werden gebruikt om de componenten, interacties en feedbackmechanismen met betrekking tot phytophthorabeheersing te beschrijven en te analyseren: 1) een literatuurstudie, 2) semigestructureerd interviews met stakeholders en 3) een modelanalyse genaamd ‘fuzzy cognitive mapping’. De resultaten lieten zien dat het gepubliceerde onderzoek zich vooral richt op agronomische praktijken, aardappelveredeling voor resistentie tegen phytophthora en chemische bestrijding. Er werden diepte-interviews afgenomen met boeren, vertegenwoordigers van veredelingsbedrijven en experts. De resultaten lieten zien dat veel verschillende stakeholders betrokken zijn bij phytophthora-beheersing en dat zij allemaal verschillende doelen en belangen hebben. Dit leidt tot verschillende soorten interacties zoals samenwerking en handel maar ook concurrentie. Boeren spelen een centrale rol in het systeem omdat zij beslissingen maken over gewasbeheer maar zij worden ook sterk beïnvloed door handelaars, veredelaars, openbare instellingen en beleid. De fuzzy cognitive map vatte de belangrijkste factoren en relaties samen die van invloed zijn op phytophthora-beheersing. De fuzzy cognitive map liet zien dat sociale en ecologische processen nauw met elkaar verbonden zijn. Ook werden verschillende terugkoppelingseffecten waargenomen. Met behulp van de fuzzy cognitive map werden drie verschillende scenario’s onderzocht. Deze scenario’s weerspiegelen beslissingen van stakeholders die phytophthorabeheersing zouden kunnen beïnvloeden. De resultaten lieten zien dat meer samenwerking tussen stakeholders en een grotere marktvraag naar resistente rassen zouden kunnen bijdragen aan een duurzame beheersing van phytophthora. Beleidsmaatregelen die het gebruik van bestrijdingsmiddelen beperken zouden daarentegen leiden tot een verhoogde ziektedruk als er geen alternatieve strategieën worden geïmplementeerd. Voor het toepassen van alternatieve strategieën is daarom maatschappelijke en institutionele steun nodig.

In Hoofdstuk 3 werd een ruimtelijk agent-gebaseerd model ontwikkeld om het gebruik van gewasresistentie bij phytophthorabeheersing te analyseren. Het model simuleert de interacties tussen het gewas en de aardappelziekte in een agrarisch landschap, beïnvloed door weervariabelen en managementstrategieën van boeren. De epidemiologische processen zijn gebaseerd op bestaande modellen en gegevens over phytophthoradynamiek. Het model werd toegepast op een landbouwgebied in Nederland (de Noordoostpolder; 596 km2) en dagelijkse weergegevens werden gebruikt als input voor het simuleren van gewasgroei en ziektedynamiek voor een periode van 36 jaar. Het model werd gebruikt om te analyseren hoe de ziektedruk, de duurzaamheid van resistentie en de aardappelopbrengst worden beïnvloed door de ruimtelijke plaatsing van een resistent ras (met een enkel resistentiegen). De resultaten toonden aan dat het verhogen van de fractie aardappelvelden met een resistent ras de infectie met phytophthora in het landschap sterk verminderde. Op de lange termijn werd de resistentie echter doorbroken door het verschijnen van een nieuwe virulente stam. De virulente stam nam geleidelijk de gehele phytophthorapopulatie over en verlaagde de gemiddelde aardappelopbrengst van velden met het resistente ras. Er werd gevonden dat zowel lage als hoge fracties van aardappelvelden met een resistent ras in een gebied de duurzaamheid van resistentie kon verhogen. Dit patroon kan worden verklaard met de verspreiding-schaalhypothese. Volgens deze theorie wordt de verspreiding gemaximaliseerd op intermediaire schalen als gevolg van interacties tussen de verspreidingsafstand en de habitatomvang.

In Hoofdstuk 4 hebben we het agent-gebaseerde model van Hoofdstuk 3 verder uitgebreid met een dimensie over de besluitvorming bij boeren. Het model werd gebruikt om de interacties tussen gedrag van boeren en de ziektedynamiek te analyseren. Het raamwerk voor de besluitvorming van boeren werd gebaseerd op een gedragstheorie en werd ondersteund met gegevens uit de literatuur en interviews met Nederlandse aardappelboeren. We veronderstelden een scenario waarbij een nieuw resistent ras (met een enkel resistentiegen) op de markt werd geïntroduceerd. Het model werd gebruikt om de adoptie van een resistent ras door boeren, en de duurzaamheid van resistentie in de loop van de tijd te analyseren. Het model reproduceerde een zogenaamde boom-bust cyclus: het percentage boeren dat het resistente ras teelde nam toe (boom) tot de resistentie werd doorbroken door de verspreiding van een virulente stam, en als reactie schakelden boeren over op andere aardappelrassen en beheersingsstrategieën (bust). Resistentiedoorbraak kwam niet voor in alle modelsimulaties en was het resultaat van interacties tussen managementstrategieën van boeren, de weervariabelen en de ruimtelijke plaatsing van aardappelrassen. Hogere kosten voor fungiciden en een hogere opbrengst of prijs van het resistente ras verhoogden de adoptie van het resistente ras. Een groot aantal boeren bleef echter het vatbare ras telen in combinatie met fungicidengebruik, wat suggereert dat samenwerking in de hele aardappelsector nodig is om structurele transformaties in ziektebeheersing te bereiken. Bovendien benadrukt het risico op resistentiedoorbraak het belang van resistentiemanagement om de duurzaamheid van resistentie te verhogen.

In Hoofdstuk 5 werd een aangepaste versie van het agent-gebaseerde model uit Hoofdstuk 2 gebruikt in workshops met gangbare en biologische boeren. Het model werd gebruikt als een leerinstrument om het inzicht van boeren over de systeemdynamiek te vergroten en om de rol van resistente rassen voor effectieve en duurzame beheersing van phytophthora te demonstreren en te bespreken. Verschillende modelscenario's werden gepresenteerd over het effect van resistente rassen en fungiciden op phytophthorabeheersing op landschapsniveau. Kwalitatieve en kwantitatieve data werd verzameld om het effect van de workshop op de perceptie van boeren over phytophthorabeheersing te analyseren. Het model toonde aan dat de volgende resistentiemanagementstrategieën effectief kunnen zijn om de duurzaamheid van resistentie te verhogen: (verminderd) gebruik van fungiciden op alle vatbare of alle resistente velden (in gangbare landbouw), het telen van een resistente ras met meerdere resistentiegenen (in plaats van een enkel gen), en onmiddellijke loofdoding van resistente velden na infectie met de virulente stam. De workshop was erg nuttig om veranderingen in percepties van boeren te analyseren. Voor de workshop waren veel boeren zich er niet van bewust dat de resistentie doorbroken zou kunnen worden. Na de workshop was een grote meerderheid van de boeren het erover eens dat stakeholders moeten samenwerken voor een effectieve en duurzame beheersing van phytophthora. Door de ziektedynamiek op landschapsniveau te analyseren, liet het model het belang van collectieve actie zien. Voor gangbare en biologische aardappeltelers werden vergelijkbare veranderingen in perceptie waargenomen voor bijna alle onderwerpen, wat aantoont dat de workshop heeft bijgedragen aan een gemeenschappelijk begrip over phytophthorabeheersing.

In Hoofdstuk 6 hebben we de belangrijkste bevindingen van dit proefschrift besproken en de methodologie geëvalueerd. Een aantal factoren en processen werden geïdentificeerd die kunnen bijdragen aan het ontwikkelen van duurzame strategieën voor de beheersing van phytophthora. We concluderen dat resistente rassen kunnen bijdragen aan duurzame beheersing, maar resistentiemanagement is vereist om de duurzaamheid van resistentie te verhogen. Om dit te bereiken is samenwerking van stakeholders in de hele aardappelsector nodig. Om de ziektedruk laag te houden en zo verspreiding van virulente stammen te voorkomen is het belangrijk dat alle boeren meewerken. Onlangs hebben stakeholders in de biologische sector afgesproken om de komende jaren over te schakelen naar 100% resistente rassen. Verder wordt verwacht dat de komende jaren nieuwe resistente rassen op de markt komen als gevolg van ontwikkelingen in de aardappelveredeling. Vanwege deze veranderingen wordt verwacht dat het areaal resistente rassen in de toekomst zal toenemen. De bevindingen uit dit onderzoek met betrekking tot resistentieduurzaamheid en resistentiemanagement zijn in dit verband zeer relevant, vooral omdat opschaling van resistente rassen het risico kan vergroten dat nieuwe virulente stammen zich verspreiden. Daarnaast beïnvloeden nieuwe ontwikkelingen zowel sociale als ecologische systemen wat het belang van een interdisciplinaire benadering benadrukt.

Om het sociaal-ecologische systeem van de aardappelziekte te analyseren, werd een verzameling van methoden gebruikt, waaronder diepte-interviews, fuzzy cognitive mapping, agent-gebaseerde modellen, scenario-analyse en participatieve methoden. Het gecombineerde en complementaire gebruik van deze methoden heeft bijgedragen aan een beter begrip van de systeemcomponenten en de interacties. Voor toekomstig onderzoek naar sociaal-ecologische systemen kan een dergelijke portfoliobenadering bijdragen aan het analyseren van deze systemen en de ontwikkeling van beleid.

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In the following sections, I switch to Dutch to address a personal note to my friends and family.

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About the author

Francine Pacilly was born on the 4th of February, 1988 in Weert, the Netherlands. Already from a young age she showed an interest in nature and after completing her secondary school education she started a Bachelor in Biology at Wageningen University. She did a specialisation in Ecology and for her Bachelor thesis she studied the risk of the fox tapeworm for humans in the Netherlands. After completing the Bachelor degree in 2010 she continued with a Master at Wageningen University in the same field. For her MSc thesis, Francine studied the ecology of ticks and infection rates with the *B. burgdorferi* bacteria, the causal agent of Lyme disease, which resulted in a publication. The project was a collaboration between the Laboratory of Entomology and Resource Ecology Group at Wageningen University, De Hoge Veluwe National Park and the Dutch National Institute for Public Health and the Environment (RIVM). Francine did her internship at the University of Hawaii and University of California Riverside where she did research on parasitic wasps together with three fellow students. This research was awarded with the Uyttenboogaart-Eliasen Stichting Thesis Award. During her studies Francine enjoyed working on societal relevant topics as well as collaborating with stakeholders. She applied for this project, which combined these interests and provided a new challenge. In 2013, Francine started her PhD project at the Farming Systems Ecology Group at Wageningen University of which this thesis is the result.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Potato late blight as a social-ecological system

Writing of project proposal (4.5 ECTS)

- Designing disease-resistant cropping landscapes using spatial models of epidemics and socio-institutional dynamics – the case of potato (*Solanum tuberosum*) and late blight (*Phytophthora infestans*)

Post-graduate courses (8 ECTS)

- Complex dynamics in human-environment systems; SENSE (2013)
- Companion modelling; PE&RC (2014)
- Summer school - individual- and agent-based modelling; TU Dresden (2015)

Invited review of (unpublished) journal manuscript (2 ECTS)

- Agronomy for Sustainable Development: disease management in agroecosystems (2016)
- Ecological Applications: an individual-based model on host-pest dynamics with implications for resistance management (2017)

Deficiency, refresh, brush-up courses (6 ECTS)

- Simulating emergence in populations and artificial societies; Information Technology Group (INF) (2013)

Competence strengthening / skills courses (2.4 ECTS)

- PhD Workshop carousel; WGS (2014)
- Scientific writing; Wageningen in'to Languages (2014)
- PhD Workshop carousel; WGS (2016)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.1 ECTS)

- PE&RC Weekend first year (2013)
- PE&RC Day (2014)

- PE&RC Day (2015)
- PE&RC Weekend last year (2016)

Discussion groups / local seminars / other scientific meetings (5 ECTS)
- Wageningen PhD symposium (2013)
- Workshop on sensitivity analysis of agent-based models (2013)
- Seminar Groningen Center for Social Complexity Studies (2013, 2014)
- Discussion group, Sustainable Intensification of Agricultural Systems (SIAS) (2013-2016)
- Workshop, social unrest among humans and animals (2014)
- Complex adaptive systems seminar: going potatoes (2014)
- Tipping points in pest management (2016)
- Frontiers in resilience research (2017)

International symposia, workshops and conferences (10.8 ECTS)
- European Association for Potato Research (EAPR); Brussels, Belgium (2014)
- European Social Simulation Association (ESSA); Barcelona, Spain (2014)
- European Social Simulation Association (ESSA); Groningen, the Netherlands (2015)
- Complex Systems Society; Amsterdam, the Netherlands (2016)
- Netherlands Annual Ecology Meeting; Lunteren, the Netherlands (2017)

Lecturing / Supervision of practicals / tutorials (8.1)
- Academic Consultancy Training (ACT) (2013)
- Systems analysis, simulation and systems management (2013, 2015, 2016)
- European Social Simulation Association (ESSA) summer school (2015)
- Agent-based modelling of complex adaptive systems (2016)

Supervision of MSc students (1 ECTS)
- Simulating potato late blight dynamics using agent-based modelling

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