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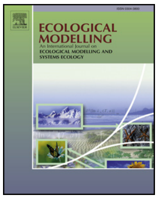

Simulating crop-disease interactions in agricultural landscapes to analyse the effectiveness of host resistance in disease control: The case of potato late blight

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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. Resistance breakdown was 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.

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.

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However, when they became more widely used, resistance breakdown occurred due to pathogen adaptation, resulting in the emergence of new virulent pathogen strains (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 an agent-based modelling approach. 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).

2. Material and methods

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).

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.

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 Fig. 1).

The model is grid based (133 × 129 cells) and the grid cells, representing an area of $200 \times 200\,m^2$ (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 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 2.1.3. and Section 2.1.7.

Since late blight development and crop growth is weather

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