



A two-dimensional stochastic model of downy mildew of radish

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Abstract

A two-dimensional stochastic model that simulates the spread of disease over space and time was recently proposed by Xu and Ridout [Xu, X.M., Ridout, M.S., 1998. Effects of initial epidemic conditions, sporulation rate, and spore dispersal gradient on the spatio-temporal dynamics of plant disease epidemics. *Phytopathology* 88, 1000–1012]. In a theoretical study, the authors showed the ability of their model to generate a broad range of disease patterns and disease progress rates. The objective of our study was to test if this theoretical approach was able to describe disease progress and the disease pattern of a specific disease, downy mildew (*Peronospora parasitica*) of radish (*Raphanus sativus* L.). Two field experiments with artificial inoculation were carried out and disease incidence and spatial pattern were assessed twice a week until disease incidence was greater than 0.25. Four model parameters were estimated by an algorithm that uses a least square regression together with an evolutionary optimisation strategy. Moran's I indices of spatial autocorrelation calculated both for measured and simulated data were significantly correlated ($\alpha = 0.05$, $r = 0.61$). Also observed variances in measurements and in simulations were closely and significantly correlated ($\alpha = 0.05$, $r = 0.95$). Thus, disease pattern (as assessed in terms of variance inflation and spatial autocorrelation) was well described by the model. The model accounted for 94% of the variation in the disease incidence data. It has, therefore, the potential to be developed into a forecast model for risk analysis and for decision support in plant protection. However, in the specific case of downy mildew on radish more experimental data are required for model validation and to parameterise the effects of environment on infection, sporulation and spore dispersal.

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1. Introduction

Models are efficient tools in quantitative epidemiology and, therefore, many have been developed to both describe and predict disease progress (Teng, 1985). The model algorithms range from single equations (van der Plank, 1963) to complex simulators that include weather generators and plant growth models (Luo et

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al., 1997). Single equation models of mean disease incidence have heuristic values (Teng, 1985); however, to understand the biological processes that govern the spread of plant disease, it is necessary to consider both spatial and temporal dynamics (Gibson and Austin, 1996). Such information is also needed to develop more accurate sampling plans and design and analyse experiments more efficiently (Turechek and Madden, 1999).

In particular, if comparisons are made between epidemics that differ in their spatial aspects, such as field size or location of initially infected plants, the interpretation of a temporal analysis should take the effects of spatial aspects into account (Xu and Ridout, 1998).

The generation of spatial pattern in stochastic models has been reviewed by Shaw (1994), who stated that many probability distributions used in the literature for describing dispersal of spores result in a more or less regular front of disease expanding out from a focus. This type of expansion has been verified in several individual cases (Zadoks and van den Bosch, 1994), but might not be suitable for all diseases (Shaw, 1994). Shaw suggests considering probability distributions where the probability does not decrease exponentially with distance, such as the Cauchy distribution. This long-tailed distribution does not form an expanding front, but generates an aggregated disease pattern (Stewart et al., 1995; Shaw, 1994). A two-dimensional stochastic model in which spore dispersal is governed by a Cauchy distribution was recently proposed by Xu and Ridout (1998). The authors carried out a thorough simulation study to analyse statistical properties of the model and showed its ability to generate a broad range of disease pattern and disease progress rates. They stated that the model was not intended to describe any specific epidemic, but it seems to be particularly suited as a fit for experimental data. This is because: (I) it reflects the important mechanisms of an epidemic, such as the rate of sporulation and spore dispersal, (II) it allows for spatial aspects, such as field size and location of initial inoculum, (III) it has only a few parameters to be estimated from experimental data, and (IV) it can be easily extended for environmental effects such as prevailing wind directions (Xu and Ridout, 2001).

The objective of this study was to test if the theoretical model suggested by Xu and Ridout (1998) was able to describe disease progress and the disease pattern of a

specific disease. For that purpose, the model was fitted to measurements from field experiments with downy mildew (*Peronospora parasitica*) of radish (*Raphanus sativus*).

2. Materials and methods

2.1. Experiments

Field experiments were carried out at the Institute of Vegetable and Ornamental Crops, Großbeeren, Germany. Radish, cv. Sirri, was sown on 25 July 1997 (data set one) and 28 September 1997 (data set two), with a plant density of 230 plants m^{-2} in a 24 m \times 24 m field.

The plants were inoculated with a suspension of *P. parasitica* conidia (10^5 conidia ml^{-1}) in the centre of the field when they reached growth stage 11 or 12 according to the developmental scale described by Hack et al. (1992); i.e., when the first or the second true leaf was unfolded. In the first experiment, 56 plants were infected and 8 plants in the second one. To improve the conditions for initial infection, the leaf wetness of inoculated plants was maintained for 24 h by a water hose with spraying nozzles. The water supply was controlled by an electric leaf wetness sensor (SW120D Surface Wetness Probe, S.W. & W.S. Burrage, Hastingleigh, UK). Field plots were irrigated at least twice a week in the afternoon to optimise conditions for the sporulation of the downy mildew. Disease incidence was assessed twice a week in the morning following the irrigation the day before by counting the number of plants with sporulating *P. parasitica* in 0.5 m \times 0.5 m sized squares. Samples were taken from 576 squares that were systematically distributed over the field (Fig. 1). Sampling was stopped when disease incidence was greater than 0.25, which occurred 16 and 26 days after inoculation in data set one and two, respectively. At the last sampling date of the first data set, only 480 squares were sampled owing to a limited labour supply. Aside from omitted fungicide treatments, crop husbandry was as by commercial practice.

2.2. Model

The model is very similar to that described by Xu and Ridout (1998). Disease progress is modelled on a rectangular grid of adjacent units. A unit in our model

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