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Linking cropping system mosaics to disease resistance durability

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ABSTRACT

Cultivar resistance plays a major role in current disease management strategies, but its efficacy is usually short-lived unless resistance deployment strategies to ensure resistance durability can be designed. Using a spatially explicit model, we evaluated cropping system mosaics that were designed by stakeholders involved in field agronomic practices to manage phoma stem canker of winter oilseed rape. We simulated pathogen population adaptation to a newly introduced major resistance gene (RlmX) to estimate the durability of the resistance under various scenarios of cropping system mosaics within a small region. Our objective was first to find descriptors of agricultural landscape that are relevant for resistance management and then to study the relationship between cropping practices applied in nearby fields and the genetic structure of the pathogen population in fields cropped with RlmX-cultivars. Key cropping practices were characterized with different metrics for several buffer sizes (100–2000 m) around target fields; and these indicators were used in linear models to predict pathogen evolution. Indicators describing local cultivar composition were very informative; adding information on tillage, but not nitrogen fertilization or fungicide treatment, could marginally increase the goodness of fit. The effects of cropping practices on resistance durability could be shown when the landscape was characterized within 500 m around RlmX-fields. We conclude that, in order to study and ultimately design landscapes promoting resistance durability against phoma stem canker, it is sufficient to take into account a relatively small portion of the landscape around RlmX-cultivars, focusing on cultivar choice and tillage practices of RlmX cultivated fields.

1. Introduction

Landscape simplification in terms of cultivated crops, linked to the historical simplification of cropping systems (Stoate et al., 2001), has resulted in agrosystems being more sensitive to pests and diseases (Meehan et al., 2011). The increase in genetic uniformity of agricultural landscapes promotes disease epidemics, favoring pathogen spread and evolution across landscapes (Stukenbrock and McDonald, 2008). In order to control pathogens, genetic control is very efficient in the short term and therefore widely used. However, specific resistance genes can be quickly overcome through the adaptation of the pathogen population, which is favored by the intensive use of a single resistance gene within cultivars grown in the landscape (Rouxel et al., 2003). The durability of specific resistance genes, i.e. the increase of gene efficacy duration, can be promoted by cropping practices such as tillage for pathogens whose inoculum resides in the soil during their life cycle (Schneider et al., 2006) and, for pathogens displaying large-scale dispersal, by optimized cultivar allocation at the landscape scale (Lo-Pelzer et al., 2010b; Skelsey et al., 2005, 2010). Therefore, strategies of resistance gene deployment as well as optimized cropping systems have to be defined at the multi-year and landscape scales for efficient and durable disease control (Aubertot et al., 2006). To assess a strategy's efficiency, spatially explicit modeling is very useful, since such scales are difficult to address experimentally (Hijmans and vanIttersum, 1996).

Phoma stem canker of Winter Oilseed Rape (WOSR), caused by *Leptosphaeria maculans*, is a typical pathosystem for which landscape characteristics, in terms of cultivars and cropping practices, influence disease spread (Aubertot et al., 2006). Today, its management relies mainly on the use of resistant cultivars, especially cultivars with specific resistance (i.e. gene for gene interaction; Flor, 1971), which are named RlmX (X is the number of the gene, currently resistances Rlm1-7 are known). Moreover, *L. maculans* ascospores are wind-dispersed over long distances (Bokor et al., 1975) and the life cycle contains year-to-year recurrence processes (Hall, 1992; Lo-Pelzer et al., 2009); therefore spatio-temporal

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patterns of crops and crop management plans have a strong influence on the disease and pathogen evolution. The spatially explicit model SIPPOM-WOSR has been designed to assess landscape-scale strategies for phoma stem canker control and improvement of specific resistance durability (Lo-Pelzer et al., 2010b).

However the analysis of such a complex model is not easy, as it contains no explicit relationship between any specific characteristic of the landscape of cultural practices and its final output, disease resistance durability. Therefore, in order to extract generic knowledge concerning the effect of cultural practices in neighboring fields on resistance durability, it is necessary to apply statistical methods to extract such relationships from simulated data. In a previous paper (Hossard et al., submitted), we showed that cultivar choice is the main explanatory variable for resistance durability on the scale of the whole landscape, but part of the variability in disease resistance durability remained unexplained for some landscape conformations. This might be because this first analysis did not take into account the landscape of cultural practices at a local scale. The same landscape composition in terms of cropping systems can lead to different spatial allocations of crops and cropping practices, i.e. agricultural landscape configurations (Dury et al., 2012), which might affect disease dynamics and pathogen adaptation to cultivar resistance, since the disease spreads between fields over a limited distance. Therefore in this paper we focused on methods allowing the local conformation of the landscape to be taken explicitly into account.

There is no consensus in the literature on the most appropriate way to describe the landscape of cultural practices and its effect on pests or pathogen populations, and a host of methods exists to compute and choose different "landscape metrics" (McGarigal et al., 2012; Boussard and Baudry, 2014; Schindler et al., 2015). For example Rusch et al. (2011) used the proportion of habitats for pollen beetles in buffers of several sizes around the studied fields while Colbach et al. (2009b) used the minimum distance between GM and non-GM maize varieties.

The objective of this paper was to test and rank different methods to describe agricultural mosaics regarding their capacity to predict the frequency of virulent pathotypes at the landscape scale. With this aim, we analyzed the effects of cropping system characteristics in the neighborhood of RlmX-fields on the durability of specific resistance used to control phoma stem canker. This was done through the identification of: (1) the most relevant metrics for characterizing cropping system mosaics (area-based, distance-based); (2) the spatial scales at which cropping practices influence pathogen population genetic evolution (from 100 to 2000 m); and (3) the most influential cropping practices (among cultivar choice, soil tillage, fertilization and pesticide use).

2. Materials and methods

2.1. Presentation of the model

We used the spatially explicit model SIPPOM-WOSR (Lo-Pelzer et al., 2010b) to simulate the effects of cropping system mosaics (composition and localization within a landscape) on resistance durability of cultivars displaying specific resistance toward phoma stem canker. The model is presented here following the O part of the ODD protocol (Overview, Design concepts, Details) for describing models (Grimm et al., 2006, 2010). Details on model equations and initialization are provided in Appendix A.

2.1.1. Model purpose

The purpose of the model SIPPOM-WOSR is to assess and rank, at a regional and multi-year scale, crop management strategies that would durably control phoma stem canker of winter oilseed rape, through the preservation of the efficacy of specific resistances.

2.1.2. Entities, state variables and scales

The model simulates the dynamics of evolution of *L. maculans* population on 16.7 km^2 over a period of 5 years at annual time steps. Two low-level entities are included in the model. The first entities are the individual fields, where the pathogen population evolves each year (Fig. 1). The considered fields are those cropped with oilseed rape. These fields are target fields for infection by spores of the pathogen agent and become, after harvest of the oilseed rape crop, source of spores for the following growing season. Individual fields are described by their location, soil type and cropping practices, including cultivar type (i.e. cultivar susceptible or not to become infected by pathogens with different avirulence genes, i.e. susceptibility to different pathotypes, and growth characteristics). The second entities are the pathogen agents, moving from one field to other ones according to their locations and wind characteristics (speed and direction) (Fig. 1).

State variables characterizing pathogen agents are the number of ascospores produced on each (source) field, the number of ascospores landing on target fields, the number of infectious ascospores (due to the interaction between the genetic structure of the ascospores and the resistance characteristics of cultivar) and the genetic structure of the pathogen population on target fields (pathotype frequencies). These variables are all unitless. State variables characterizing individual fields are related to crop growth: Leaf Area Index (unitless), number of leaves (unitless) and biomass ($g\,m^{-2}$). High level state variables, computed on an annual time step, are the size and structure of the pathogen population and the relative yield losses (all unitless) at the landscape scale, resulting from individual fields' states (Fig. 1).

Sub-models are represented by rectangles, weather and input data by diamonds, technical inputs by ovals, initialization parameters by trapeziums, and model outputs by rounded squares. State variables are shown in italics. ETP: evapotranspiration (mm).

2.1.3. Process overview and scheduling

The model is composed of five sub-models representing processes (Fig. 1): (1) primary inoculum production, (2) ascospores dispersal, (3) genetic (compatibility between source and target fields), (4) WOSR growth and (5) WOSR infection by *L. maculans* and subsequent yield losses. The first process is the production of primary inoculum, determining the number of ascospores, beginning each year at WOSR harvest until winter start for each field (Fig. 2). Then WOSR crop growth is simulated for each concerned field, from sowing to winter start; Leaf Area Index and number of leaves are calculated every day from emergence to winter start. In the same time, ascospores are dispersed from source to target fields, and the number of infectious ascospores and subsequent crop infection is simulated at a daily time step for each field. At winter start, biomass and pathotype frequencies are simulated for each field (see Fig. 2). At the end of each year, high scale variables (model outputs) are computed from individual field data (structure and size of the pathogen population, relative yield losses).

2.1.4. Inputs

The main model inputs are the field map (spatial distribution of fields), soil and climatic data (Fig. 1), initial genetic structure of the pathogen population and its location, and the spatially distributed cropping systems, providing details on location of WOSR fields and their cultivation techniques (sowing date and density, cultivar, nitrogen fertilization, fungicide use, tillage practices).