

Linking cropping system mosaics to disease resistance durability

Laure Hossard, Marie Gosme, Véronique Souchère, Marie-Helene Jeuffroy

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Corresponding Author: Dr. Laure Hossard, Ph.D

Corresponding Author's Institution: INRA

First Author: Laure Hossard, Ph.D

Order of Authors: Laure Hossard, Ph.D; Marie Gosme, Ph.D; Véronique Souchère, Ph.D; Marie-Hélène Jeuffroy, Ph.D

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 (100-2000m) 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 meters 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.

Highlights

We characterized landscapes of cropping practices with 3 metrics and 9 buffer sizes These metrics were used to predict pathogen evolution against cultivar resistance Best predictors of resistance durability were based on cultivar and tillage practices Characterizing the landscape within 500m was sufficient to provide good estimations Considering distance between source and target fields gave more stable estimations Linking cropping system mosaics to disease resistance durability

Laure Hossard, Marie Gosme, Véronique Souchère, Marie-Hélène Jeuffroy

L. Hossard (Corresponding author)

INRA, UMR211 Agronomie; AgroParisTech, UMR211 Agronomie; F-78850 Thiverval-Grignon, France

Present address: INRA, UMR0951 Innovation; F-34060 Montpellier, France

Email laure.hossard@supagro.inra.fr; Phone +33 (0)4 99 61 20 19 ; Fax : +33 (0)4 67 54 58 43

Marie-Hélène Jeuffroy, Marie Gosme

INRA, UMR211 Agronomie; AgroParisTech, UMR211 Agronomie; F-78850 Thiverval-Grignon, France

L. Hossard, V. Souchère

INRA, UMR1048 SADAPT; AgroParisTech, UMR1048 Sadapt; F-78850 Thiverval-Grignon, France

Abstract

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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

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under various scenarios of cropping system mosaics within a small region. Our objective was

genetic structure of the pathogen population in fields cropped with RlmX-cultivars. Key cropping practices were characterized with different metrics for several buffer sizes (100-2000m) 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 meters 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.

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 (Lô-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 van Ittersum, 1996).

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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, *Leptosphaeria maculans* ascospores are wind-dispersed over long distances (Bokor *et al.*, 1975) and the life cycle contains year-toyear recurrence processes (Hall, 1992; Lô-Pelzer *et al.*, 2009); therefore spatio-temporal 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 (Lô-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 55 final output, disease resistance durability. Therefore, in order to extract generic knowledge concerning the effect of cultural practices in neighbouring 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 60 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 *et al.*, 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 (Lô-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 towards 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.

Model purpose

95 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.

Entities, state variables and scales

The model simulates the dynamics of evolution of *Leptosphaeria maculans* population on 16.7 km² over a period of five 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 (Figure 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.

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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) (Figure 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 (Figure 1).



Figure 1. Flow chart of the model SIPPOM-WOSR (a Simulator for Integrated Pathogen Population Management).

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).

125 Process overview and scheduling

The model is composed of five sub-models representing processes (Figure 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 (Figure
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 Figure 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).



140 Figure 2. Yearly scheduling of state variables.

Inputs

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The main model inputs are the field map (spatial distribution of fields), soil and climatic data (Figure 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).

2.2. Presentation of the studied area

The study was conducted in an area located in the Picardie administrative district (NUTS 2) of France (Figure 3). Currently this district is characterized by a WOSR acreage representing

150 9.6% of the arable land (Agreste, 2014), and diverse crop management plans (e.g. tillage

practices and cultivars; source: SSP Enquêtes Pratiques Culturales 2006). Because of very different agricultural contexts related to soil features, three regions (NUTS 3) were defined within the study area: Tardenois (T), Oise (O) and Somme (S), which correspond to different cropping systems. Since regions did not differ in terms of field sizes and shapes, the same field map (17 km², composed of 158 fields and digitized from an actual landscape located between 49°25'54- 49°28'51N and 02°09'13- 02°15'13E) was used for these three regions, with the same local climatic data provided by Meteo France.



160 Figure 3. Location (A) and simulation support map (B) of the Picardie district, i.e. field plans presenting one year-random WOSR allocation (3 realizations) with 29% of the areas cropped with WOSR. Black fields contain WOSR.

Predicted future crop management systems

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Possible future cropping systems for each region have been designed with local stakeholders (farmers, crop collectors, crop breeders, extension and advisory services, representatives of technical organizations). They were designed in two steps: (1) identification of likely future agricultural contexts (two future contexts, A: "Environmental scenario", with a decrease in WOSR due to weeding issues; and B: "Economic scenario", with a competitive price advantage for WOSR, leading to an increase in WOSR; see Table 1), and (2) design of

170 cropping systems adapted to each of these contexts (Hossard *et al.*, 2013; Table 1). As the effect of a change in the agronomic and socio-economic context on farmers' decisions cannot be precisely predicted, stakeholders chose to define several possible outcomes (first in terms of the proportion of WOSR in the landscape and of the proportion of resistant cultivars among WOSR crops, then in terms of nitrogen fertilization, tillage, fungicide use or sowing date and 175 density) for each future context. We used these scenarios to generate virtual landscapes: crops were randomly assigned to fields in our field map according to the crop proportions defined in the scenario. Then WOSR-cropping practices (cultivar, type of tillage, autumn nitrogen fertilization, fungicide application and sowing time and density) were randomly applied to oilseed rape fields according to the respective proportions defined in the scenario, each

180 practice being treated independently from the others (Table 1).

As the same scenario (landscape composition in terms of crops, cultivars and cropping practices) could lead to many different spatial configurations, each scenario was simulated three times with different (random) spatial allocation of crops and crop management systems (hereafter called scenario realizations) (Figure 3). Each scenario spatial realization was then used to simulate disease dynamics and evolution for five years (one year of initialization (year 1) and four years included in the analysis (years 2 to 5)). Finally, two climatic datasets were used: the current one (real data for years 2003-2008) vs. one that is *a priori* favorable to phoma stem canker epidemics (i.e. replicate of one-year data with higher autumn temperatures and rainfall).

190 Table 1. Characteristics of the cropping system scenarios, defined on the scale of the whole landscape. Several figures in one cell (separated by

"or") indicate that several options were tested.

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Trend	WOSR (%) ^a	RlmX/non-RlmX Cultivars ^{b, c} (%)	Nitrogen fertilization ^b (%)	Tillage ^{b, d} (%)	Fungicide ^b (%)	Mean sowing time ^b (date)	Mean sowing density ^{b, e} (s m ⁻²)	Number of scenarios ^f
A T 10 15	10	15/85	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
A.T.20 15	20	15/85	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
 A.T.10_40	10	40/60	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
A.T.20_40	20	40/60	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
A.T.10_60	10	60/40	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
A.T.20_60	20	60/40	40	2SB or 50% 1SB/ 50% 2SB or 50% 2SB/50% 3SB	10	27.08 or 20.08	55 or 25	72
B.O.15_15	15	15/85	20	67% 2SB / 33% 1SB	50 or 10	26.08	45	12
B.O.20_15	20	15/85	20	67% 2SB / 33% 1SB	50 or 10	26.08	45	12
B.O.25_15	25	15/85	20	67% 2SB / 33% 1SB	50 or 10	26.08	45	12
B.S.15_6	15	6/94	60	RT+SB	20 or 10	20.08	32	12
B.S.20_6	20	6/94	60	RT+SB	20 or 10	20.08	32	12
B.S.25_6	25	6/94	60	RT+SB	20 or 10	20.08	32	12

^apercentage of oilseed rape in the cropped area; ^bpercentage of the WOSR area receiving the considered practice; ^cproportions of RlmX/ non-RlmX cultivars; ^dpercentage of the WOSR area receiving different tillage practices, SB: Stubble breaking; RT: Rotary harrowing ; ^eexpressed in seeds per square meter (s.m⁻²); ^fnumber of scenario realizations resulting from the combination of the previous columns, including the two tested climatic datasets and the three random spatial allocations of crops and cropping practices in fields (e.g. for A.T 10 15: 3 tillage options x 2 sowing time options x 2 sowing density options x 2 weather options x 3 scenario/spatial realizations).

2.3. Studied variables and metrics

The output used for estimation of resistance durability was the fraction of virulent pathotypes on RlmX-gene (avrlmX), commonly used by pathologists (e.g. Brun et al., 2010; Rouxel et al., 2003). This fraction was computed at the end of the five-year simulation and over the whole landscape. RlmX-cultivars are the ones where resistance breakdown may occur (the 200 absence of competition with non-RlmX pathogen strains allow the buildup of RlmX inoculum in formerly resistant fields). Thus it is their local environment that determines the early invasion of the population by resistant strains and therefore the onset of resistance breakdown. As a result, the local landscape was characterized in circular buffers around each field cultivated in year y with the RlmX-cultivar (target field). Given the year-by-year 205 recurrence of the cycle of phoma stem canker, the fields that produce inoculum (source fields) are the fields cultivated with WOSR in year y-1. Since the effect of cropping practices on disease resistance durability depends on the cultivar type on which they are applied (Lô-Pelzer et al., 2010a), fields cultivated with WOSR in year y-1 were characterized by the combination of their genetic makeup (presence of the resistance gene) and each of the 210 relevant cropping practice (ploughing, which buries the infectious residues, autumn nitrogen fertilization, which increases leaf area and thus spore capture, and fungicide application, which protects from infection). We did not consider sowing time and density as their range was not large enough to significantly affect disease resistance durability. Since stakeholders considered cropping practices independently of each other, no interactions between practices 215 were included (except between cultivar choice and each of the other practices considered). Therefore independent variables were computed for each type of target field separately, with eight types of fields: with or without the resistance gene, ploughed with or without the resistance gene, fertilized with or without the resistance gene and fungicide-treated with or

220 without resistance gene. Independent variables were used to determine, if appropriate, which (single) cropping practice would be of most interest to explain resistance durability.

Three metrics were used to characterize the landscape around target fields: area-based, density-based and distance-based metrics (Table 2). Area-based metrics were computed as the sum, over all years, of the sum over all target fields of the acreage of source fields of a given

- type A, divided by the total acreage of the buffer. Density-based metrics were computed as the sum, over years, of the sum, over target fields, of the sum of acreage of source fields of type A divided by the acreage of the target field, to account for the importance of target fields on regional outputs. Finally distance-based metrics were computed, for each target field j, as the area of each source field i of type A within the buffer divided by the squared distance between source field i and target field j. As this last metric is meant to represent a risk factor, it was not summed over fields and years but the maximum was taken. These metrics were computed for nine buffer radii, measuring 100m and then from 250m to 2000m by steps of 250m. The combination of one specific practice applied on a specific cultivar type and characterized with a specific metric within a specific buffer provides one single indicator that
- will be used for further analyses.

Table 2. Subsets of source fields (oilseed rape fields in year y-1) and metrics used to describe the local landscape around target fields (oilseed rape fields in year y), as a function of the considered cropping practices.

Metrics	Area-based	Density-based	Distance-based
A_j is the subset of source fields within buffer j that had:	$\sum_{y} \sum_{j} \frac{\sum_{i \in A_{j}} s_{i}}{\sum_{i \in buffer_{j}} s_{i}}$	$\sum_{y} \sum_{j} \frac{\sum_{i \in A_{j}} s_{i}}{s_{j}}$	$max_{y}max_{j}\sum_{i\in A_{j}}\frac{S_{i}}{d_{ij}^{2}}$
Cultivar:	RlmX or Non-RlmX	RlmX or Non-RlmX	RlmX or Non-RlmX
Deep tillage after:	RlmX or Non-RlmX	RlmX or Non-RlmX	RlmX or Non-RlmX
Autumn nitrogen on:	RlmX or Non-RlmX	RlmX or Non-RlmX	RlmX or Non-RlmX
Fungicides on:	RlmX or Non-RlmX	RlmX or Non-RlmX	RlmX or Non-RlmX

 Σ indicates a sum, max indicates the maximum, the subscripts indicate summation over years (y, from 2 to 5), source (i) and target (j) fields, s_i indicates the acreage of field i, d_{ij} indicates the distance between fields i and j.

Design of scenario analysis

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In order to separate the effect of the overall proportion of landscape cropped with RlmX-245 cultivars from the local effect of cropping practices, which is the focus of this paper, we grouped the scenarios generated by the stakeholders into "future trends" with a constant overall proportion of RlmX cultivars in the landscape within each trend. One trend was thus defined as the combination of one future context in one region, one proportion of WOSR and one proportion of RlmX cultivars among WOSR cultivars. Trend information was 250 summarized in the trend's name, with the 1st letter indicating the considered future context, the second letter the region, the 1st number the proportion of WOSR within the landscape and the last number the proportion of RlmX cultivars (Table 1). Due to the different modalities for each cropping practice within a trend, and their multiple combinations, the two weather time

series and the three scenario spatial realizations obtained for each scenario through the random allocation of crops and cropping practices, from 12 to 72 scenarios, were grouped within one trend. The analysis made use of this variability to examine the relationship between several descriptors of the local landscape surrounding RlmX-target fields and the durability of disease resistance.

Statistical analyses

Simple linear models were used to assess the effects of indicators (taken one at a time) on the 260 avrlmX allele proportion in the pathogen population at the end of the simulation (Equation 1). The indicators are the combinations of one specific metric (area-, density-, or distance-based), one specific cropping practice (cultivar, tillage, fertilization or fungicide) on a specific cultivar type (RlmX or non-RlmX) within one specific buffer (100-2000 m) (Table 2). 265 Regressions were performed for each trend and indicator separately (Equation 1), individuals being each scenario spatial realization (e.g. 72 for trend A.T 10 15, see Table 1). Our objective was not to precisely estimate the regression coefficients, but rather to assess the ability of a given indicator to explain resistance durability in a wide diversity of possible future situations. Thus we studied the performance of indicators by considering simultaneously all models based on this indicator, and we considered the percentage of 270 significant regressions within those using this specific indicator. The performance of each indicator was considered acceptable when at least 50% of the regression slopes using this specific indicator were significant (p<0.05). For each linear regression line, the residuals were checked for symmetry and normality, as well as independence from fitted values. Models were compared based on the value of R^2 as well as the significance of the t-test on the 275 estimate of the slope (p<0.05). Akaike Criterion (AIC) was also used to compare each model (1) with the constant model (no explanatory variable) and (2) the other models (based on

different indicators) within each trend. AIC and R^2 resulted in similar conclusions in terms of indicator performance (data not shown). Analyses were carried out with R software (R Development Core Team, 2009).

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(Equation 1) avrlmX = a+b.Indicator, where i is the treatment (scenario spatial realization) within a trend, avrlmX is the proportion of virulent pathotypes on RlmX-cultivars at the landscape scale, a is the intercept, b is the effect of the explanatory variable (Indicator), and Indicator is the combination of one specific cropping practice characterized with a specific metric on a specific cultivar type within a specific buffer.

3. Results

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3.1. Landscape scale

Model simulations of the final avrlmX (virulent pathotype) proportion in the population displayed a wide variability among future trends (Figure 4). The ranking of trends highlighted

the frequency over the whole landscape of RlmX-cultivars (resistant) as the main variable 290 affecting the proportion of virulent pathotypes at the landscape scale: the higher this frequency, the quicker the breakdown of RlmX-gene, whatever the other practices. The interscenario variability of simulated avrlmX within trends varied between 5% and 33%; and was very low with a high proportion of RlmX-cultivars (60%). The intra-scenario variability within trends, due to cultivar and cropping practice spatial allocations, ranged up to 14% of 295 avrlmX. The variability of simulated avrlmX due to spatial allocations of crops and cropping practices (i.e. intra-scenario variability) thus represented a large part of within-trend variability (inter-scenario). For a specific fraction of RlmX-cultivars in a specific region (S, O and T), the variability between spatial allocations decreased as the fraction of cropped WOSR 300 increased (Figure 4).



Overlaid in blue (right-hand y axis) are the standard deviations, among the three scenario realizations, of the final avrlmX proportion Total number of scenario realizations is indicated at the top of each trend.

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When fitting a linear model on the final proportion of the virulent pathotype (avrlmX) over the whole landscape against an indicator based on the local landscape around each target field, the general performance of indicators was acceptable for landscapes with 3% and 8% of RlmX-cultivars (WOSR fraction * RlmX fraction) over the whole landscape. This performance decreased for landscapes with very low or very high fractions of RlmX-cultivars (less than 2% and equal to 12% respectively) (Table 3). These situations were the ones where the inter- and intra-scenarios' variability were the lowest (Figure 4).

Table 3. Percentage of significant slopes considering all cropping practices, all metrics and buffer sizes for each future trend and source field (RlmX vs. non-RlmX).

Trend	Proportion of RlmX- cultivars (%) ^a	RlmX source fields ^b	non-RlmX source fields ^b	Total ^c
B.S_15_6	0.9	51	98	74
B. S_20_6	1.2	11	27	19
B.S_25_6	1.5	48	41	44
A.T_10_15	5 1.5	0	2	1
B.O_15_15	5 2.25	42	41	41
B.O_20_15	5 3	29	73	51
A.T_20_15	5 3	37	56	47
B.O_25_15	3.75	56	82	69
A.T_10_40) 4	40	69	55
A.T_10_60) 6	92	74	83
A.T_20_40) 8	100	71	86
A.T_20_60) 12	0	0	0

Percentage of significant slopes (%)

315 ^aCalculated as the landscape fraction cropped with Winter Oilseed Rape (WOSR, %) multiplied by the fraction of WOSR cropped with RlmX-cultivars (RlmX, %) at the landscape scale ; ^bProportion based on 108 regressions (3 metrics x 4 cropping practices (cultivar type, tillage, nitrogen fertilization and fungicide) x 9 buffers for trends A.T and B.O, and 81 for trend B.S -as only 3 cropping were tested (only one tillage option here) ; ^cConsidering both RlmX and non-RlmX source fields, i.e. 216 regressions for trends A.T. and B.O and 162 for B.S.

When considering all types of practices and future trends, no buffer size clearly appeared as the most relevant (Figure 5; Appendix B). The most explanatory buffer size differed between the two types of cultivars grown in source fields, i.e. cultivars with or without RlmX (RlmX vs. non-RlmX respectively). When considering RlmX-cultivars as source fields, the performances of indicators to explain simulated avrlmX decreased or stabilized when the
buffer size exceeded 250m. When considering non-RlmX source fields, the most explanatory indicators were found for a buffer size of 1250m. For both types of source field, highly

explanatory indicators were found for buffer sizes between 100 and 500m, with indicators providing 53 and 64 % of significant slopes for RlmX and non-RlmX source fields respectively (Figure 5).



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Figure 5. Percentage of significant slopes considering all cropping practices and all trends for each of the three metrics as a function of buffer size.

Number of regressions is indicated for each metric (number of trends (12 in total) x number of cropping practices (3 practices for the 3 trends B.6_S_15, B.6_S_20 and B.6_S_25 (only one tillage option) and 4 for the 9 other trends): 3x3 + 4x9 = 45).

For trends displaying a landscape fraction of RlmX-cultivars (WOSR fraction * RlmX fraction) between 3 % and 4 %, the indicators based on non-RlmX source fields were the most explanatory of resistance breakdown. The indicators based on RlmX-fields performed better for trends with a landscape fraction of RlmX-cultivars between 6 and 8% (Table 3). The performance of indicators was consistent between the two types of cultivars on field sources within buffers (data not shown).

Area- and density-based metrics explained simulated virulent pathotype (avrlmX) in ways that differed between buffer sizes, unlike distance-based metrics that stabilized for buffer

345 sizes of 500m or more (Figure 5). Since this last metric weights source field areas according to their distance to the target field, distant fields, which are included only in large buffers, will have a small impact on the result unless their areas are very large, so it is not surprising that buffer size has no effect for large buffers. This stabilization occurs as soon as buffers are large enough to encompass all types of source field (e.g. with and without the studied practice)

350 (data not shown). Performance and ranking of the three metrics also differed according to the type of cultivar that was considered as the source field. For both types of cultivar in source fields, area-based indicators were the most explanatory, although not at the same buffer size nor for all buffer sizes (Figure 5).

3.3. Effect of cropping practices

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355 The ranking of cropping practices that were the most influential on simulated specific resistance durability was not consistent between regions and trends, whatever the buffer size and metric used or the type of source field considered (data not shown). Considering additional information on tillage practices yielded slightly better correlations between the indicators and RlmX breakdown than considering only the type of cultivar (Figure 6; Appendix B). On average, considering tillage information additionally to cultivar type

increased the percentage of significant slopes by about 4 points. Simulated avrlmX values increased significantly with the decrease in RlmX source fields with deep tillage practices. For all buffer sizes, adding information on nitrogen fertilization was not more explanatory for simulated avrlmX than considering cultivar alone. Considering source fields that were sprayed with fungicides during the autumn was the indicator least correlated with avrlmX proportion in the pathogen population, performing even less well than the characterization of cultivar type only.



Buffer of 500m

Figure 6. Percentage of significant slopes considering all trends, all types of source field andthe 500m buffer size for the three metrics for each cropping practice characterizing source fields.

Number of regressions is indicated in the bottom part of the graph for each cropping practice, i.e. 2 cultivar types x 9 or 12 trends depending on the considered practice (i.e. tillage was not tested in the three trends $B.6_S_15$, $B.6_S_20$ and $B.6_S_25$).

375 4. Discussion

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In this study, we analyzed how to characterize agricultural mosaics for phoma stem canker management, i.e. which metrics, buffer sizes, source fields and cropping practices could be

used as indicators to assess the influence of local cropping practices on Leptosphaeria maculans genetic evolution towards breakdown of a specific resistance gene RlmX. We showed that resistance durability of a specific resistance gene can be, in most cases, explained 380 by cultivars and possibly tillage practices applied on them, in a small area around the fields grown with the specific resistant cultivar, as indicated by the significant coefficient of determination of the linear regressions. Thus, looking at a small area in detail and distinguishing between cultivars when examining cropping practices provided information on pathogen population evolution towards RlmX adaptation that remained hidden when cropping 385 practices, including cultivars, were characterized on the scale of the whole landscape (Hossard et al., submitted). In this previous study, tillage practices, for instance, were never significantly correlated with final avrlmX values, which is not the case in this study. Characterizing small areas of the environment by means of detailed cropping system 390 characteristics in landscapes differing in host crop frequency has proved to be useful when addressing issues concerning seed, insect or spore dispersal (e.g. Rusch et al., 2011). However, up to now, such studies had never addressed disease resistance durability when faced with realistic future cropping practices. Our study could provide a basis for such assessments in order to highlight the practices and spatial scales that should be addressed in future possible contexts. 395

No single metric tested in our study gave consistently the best prediction: sometimes it was a simple cultivar proportion, but more often it was a metric based on the ratios of the area of source to target fields or on the distance between source and target fields. However the metrics weighting the area of the considered source fields with the distance between source and target fields were the most stable. This difficulty in highlighting a single metric, in the studied agricultural landscapes, could be linked with (a) the relatively high heterogeneity of

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the cropping systems assessed in this study, (b) the fact that we used real-world landscapes (with heterogeneous field areas and shapes) and finally (c) the random allocations of crop, cultivar and cropping practices among fields. This reveals the complexity of spatial and temporal interactions occurring within a small area, and the need to account not only for 405 minimum distances between source and target fields, but also to take into account all the important characteristics of the local landscape surrounding avrlmX-fields. Such a landscape approach has proved to be useful to characterize other aspects of crop disease management, e.g. regional population sizes or yield losses (Hossard et al., 2013; Skelsey et al., 2009) or observed levels of quantitative resistance (Papaix et al., 2011). Disease management by 410 cropping practices and cultivar deployment should thus be considered both on the scale of the whole landscape and on smaller areas for effective strategy design. In our study, at the whole landscape scale, the proportion of resistant cultivars provided relevant information on the range of virulent pathotypes on resistant RlmX-cultivars for risky situations (high proportion of RlmX-cultivars at the landscape scale), allowing a first ranking of the scenarios proposed 415 by the stakeholders. The characterization of other cropping practices within small areas (e.g. tillage in buffers of a hundred meters) allowed us to further discriminate between scenarios within these ranges. The precision of these ranges increased with the absolute frequency of RlmX cultivars included in the buffers (i.e. WOSR(%) x RlmX(%)): the breakdown of a qualitative resistance gene for phoma stem canker would then be better predicted in 420 landscapes with high proportions of WOSR and/or cultivars with RlmX-gene. Fortunately, such situations, with a higher presence of RlmX-cultivars and probably more homogeneously distributed in the landscape, are more risky and are the ones where management strategies would be the most useful.

- To manage resistance to phoma stem canker, Gladders *et al.* (2006) suggested local strategies, such as isolation distances between crops/cultivars, to be adopted by individual farmers or groups of farmers. For these authors, such strategies could be used if the required isolation distances are small enough (0.5-1 km). These distances are consistent with experimental studies, suggesting a 500m-isolation distance (Marcroft *et al.*, 2004). This scale may indeed be small enough for farmers to be able to choose cropping practices suited to their agricultural environment. In our study, using small buffers (100-500m) for characterizing the local cropping practices always provided good estimates of the final avrImX proportion, although in some cases the best results were obtained with large buffers, i.e. more than 500 m.
- Implementing isolation strategies however requires each farmer to know his/her neighbours' practices. At a regional scale, it would require wider collaboration between local stakeholders 435 (seed providers, agricultural advisers, farmers). In the case of Genetically Modified (GM) maize, where similar "segregation" strategies have been advocated, Coleno et al. (2009) showed the potential impacts that the crop collector could have, by dedicating silos to specific cultivars. So it would be important to include this type of stakeholder when designing durability management strategies influencing the spatial allocation of cultivar and/or cultural 440 practices. For these strategies to be implemented, it would be necessary (1) that the studied pathogen frequently causes high economic losses, so that local stakeholders are willing to take drastic control measures, and (2) that the local landscape governance permits it (Byrne and Fromherz, 2003): the local advisers have to provide consistent recommendations and all seed providers must define their strategies in collaboration with the others (Coléno, 2008). Another 445 option would be to design policies that would enforce constraints on the quality of agricultural production, which would result in the farmers adopting the desired cultivar allocation within a small area. The latter option has been suggested to ensure coexistence between GM and non-

GM crops through isolation distances, using purity thresholds for selling grain maize (Colbach *et al.*, 2009a).

Determining rules for cropping system composition and allocation for disease management could benefit from a local approach, taking into account landscape characteristics. To design sustainable crop protection strategies, cropping practice interactions could be investigated. In particular, cropping practices could differ for cultivars with and without RlmX specific resistance, e.g. deeper tillage on RlmX-cultivars. This would preserve resistance (Lô-Pelzer et 455 al., 2010b), but this effect needs to be confirmed and quantified, especially in terms of buffers within which those practices should be applied to favour resistance durability. However, optimizing cropping practices for one objective (e.g. phoma resistance durability) might lead to undesirable effects on other pests (e.g. mouldboard ploughing is advised for phoma control (Schneider et al. 2006) but it reduces the population of natural enemies of pollen beetle 460 (Rusch et al. 2011). Therefore integrated management of resistance durability requires taking into account not only individual practices but also their interactions as well as their unintended effects on other important pests of the crop. Our study provides insights on the metrics, cropping practices and scales to be considered for phoma stem canker resistance management, as a first step towards multi-pest management. 465

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