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SIPPOM-WOSR: A Simulator for Integrated Pathogen POPulation Management of phoma stem canker on Winter OilSeed Rape: II. Sensitivity analysis

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Abstract

SIPPOM, a simulator for integrated pathogen population management, has been developed to assess and rank Integrated crop management (ICM) strategies, at the regional scale. The input variables are weather data, soil characteristics, the description of cropping systems (crop sequence and winter oilseed rape crop management) and their spatial distribution, plus the initial size and genetic structure of pathogen populations. Here, we use SIPPOM to simulate phoma stem canker severity, the genetic structure of the pathogen populations, and the yield loss caused by the disease. Sensitivity analysis is conducted to quantify how strongly state variables (sub-model output variables) respond to variations in parameters. The results indicate which parameters need to be more accurately estimated, and it elucidates the steadiness of the rankings of contrasting control strategies under various weather conditions when parameters were varied. Due to the complexity of SIPPOM, the scope of this work was limited to a sensitivity analysis of each sub-model independently. Three values of each parameter were tested under various environmental conditions and crop management according to their expected or known effects on disease and yield. Qualitatively speaking, variations in input variables and parameters provided sub-model output variables that behaved as expected by experts. Parameters with the greatest effect on state variables and that need to be estimated more accurately are for instance those related to pseudothecia maturation and disease severity index estimates. Improvements are foreseen (*e.g.*, the calculation of both the number of phoma leaf spots and the severity disease index). Because the ranking of the simulated control strategies remained steady, despite large variations in the simulated variables linked with variations in parameters, the sensitivity analysis shows that the model, as it stands, can be used to compare and rank ICM strategies with respect to their effectiveness. Possibilities of a sensitivity analysis of the overall model are discussed.

Keywords: Blackleg, Integrated crop management, Modelling, Sensitivity analysis, Parameters

1. Introduction

Agricultural research is currently investigating alternative cropping systems for pest management to limit the use of pesticides in the field and preserve the efficiency of control methods over time (Tilman et al., 2002, Aubertot et al., 2005). Integrated Pest Management (IPM) combines different control methods (chemical, genetic, cultural, biological, and physical) to meet economical, ecological, and toxicological requirements (IOBC-SROP, 1973). In the case of disease management, genetic resistance, the main control method, is known to lose its efficiency over time because pathogen populations quickly adapt to specific resistance genes under selection pressure, sometimes leading to a complete loss of efficacy within just a few years (*e.g.*, Rouxel et al., 2003). To prolong resistance, it is necessary to reduce the selection pressure exerted on pathogen populations by applying a suitable strategy for the spatial and temporal use of cultivars (McDonald and Linde, 2002), while, at the same time, it is necessary to reduce the size of pathogen populations by combining cultural and chemical control methods (coined ‘Integrated Avirulence Management’ by Aubertot et al., 2006a).

In the case of airborne diseases, the dispersal of inoculum often exceeds field boundaries. In addition, many diseases are polyetic. Rather than approaching the issue from the often used field and crop cycle scales, designing control strategies at a regional and multi-year scale should be further investigated (Aubertot et al., 2006a). SIPPOM-WOSR, a simulator for integrated pathogen population management for winter oil seed rape (Lô-Pelzer et al., 2010), has been developed to assess and rank Integrated crop management (ICM) strategies,

at these scales, accounting for cultural practices, cultivar choice, and chemical control according to their ability to bring phoma stem canker under control while preserving the efficiency of specific resistances. The model simulates the disease severity and the genetic structure of this pathogen population (in terms of pathotype frequencies) in each field of a given region, as well as yield, gross margin, and environmental cost of cultural practices applied to manage the crop and to control the disease.

Sensitivity analysis of a model aims at determining how sensitive the outputs are to variability in any one of several elements, such as the values of the parameters or the input variables (Monod et al., 2006). In order to improve the predictive quality of a model, Ruget et al. (2002) and Makowski et al. (2006) emphasized the importance of pinpointing the parameters that need to be estimated with a higher precision. In the case of complex models such as SIPPOM, which has 316 parameters (L  Pelzer et al., 2010), a sensitivity analysis to variations in parameters is particularly useful as the estimation of some parameters can require specific experiments that are time-consuming and often difficult to set up (Makowski et al., 2006). Moreover, the aim of SIPPOM is to rank strategies that would control phoma stem canker. Despite any uncertainty in the estimations of parameters, the ranking of strategies has to be stable when parameters are varied if the model is to be used to this end. A sensitivity analysis to input variables in order to identify which crop practices impact more outputs and to select for ICM strategies (e.g., Breukers et al., 2007) is not to be neglected; however, given the complexity of SIPPOM, the sensitivity to parameters is an issue in and of itself.

The two objectives of the sensitivity analysis to variations in parameters that is presented here were (i) to pinpoint the parameters that need to be estimated with a higher precision and (ii) to test the steadiness of the rankings of contrasting control strategies under various weather conditions when parameters were varied. In the first part of this paper, the structure of SIPPOM-WOSR is briefly described and the method used to conduct an independent sensitivity analysis of each sub-model is detailed. This entails the parameter values, the management strategies and weather conditions in addition to the output variables. Parameters that need to be estimated with a higher precision are identified and discussed, as well as the behaviour of each sub-models depending on contrasting input variable values. Finally, the next step, a sensitivity analysis of the overall model to input variables, is evoked.

2. Materials and methods

2.1. Description of the SIPPOM-WOSR model

The SIPPOM-WOSR model has been described in detail by L  Pelzer et al. (2010). It is composed of five sub-models (Fig. 1).

The primary inoculum production sub-model simulates the primary inoculum production of *Leptosphaeria maculans*, the causal agent of phoma stem canker. Pseudothecia mature on stubble left on the soil surface after harvest and produce ascospores, the primary inoculum (Hall, 1992). This sub-model calculates, between the harvest of the crop in the previous season and the beginning of winter in the given season, (i) the impact of tillage on vertical displacement of stubble in soil (Schneider, 2005), (ii) the subsequent potential density of pseudothecia on stubble present on the soil surface, and (iii) the effect of climate on pseudothecial maturation and the release of ascospores (Aubertot et al., 2006b). The quantity of released ascospores also depends on the severity of the disease in the previous year (L  Pelzer et al., 2009a, L  Pelzer et al., 2009b).

The dynamic crop growth sub-model simulates the development stages and the growth of the crop from emergence to the end of winter, under the influence of weather and soil conditions and cultural practices, such as sowing date and sowing density or nitrogen management (impacting the leaf area that ultimately determines the interception of ascospores; Aubertot et al., 2004a). The attainable yield in each field is also simulated by this sub-model.

The dispersal sub-model simulates the flow of ascospores in the region. Mature ascospores are released after a rainfall event, and then wind-dispersed over several kilometres (West et al., 2001). The number of ascospores that each WOSR field is likely to receive in the region is thus quantified (Diggle et al., 2002). The model is spatially explicit using a 50 m \times 50 m-pixel raster.

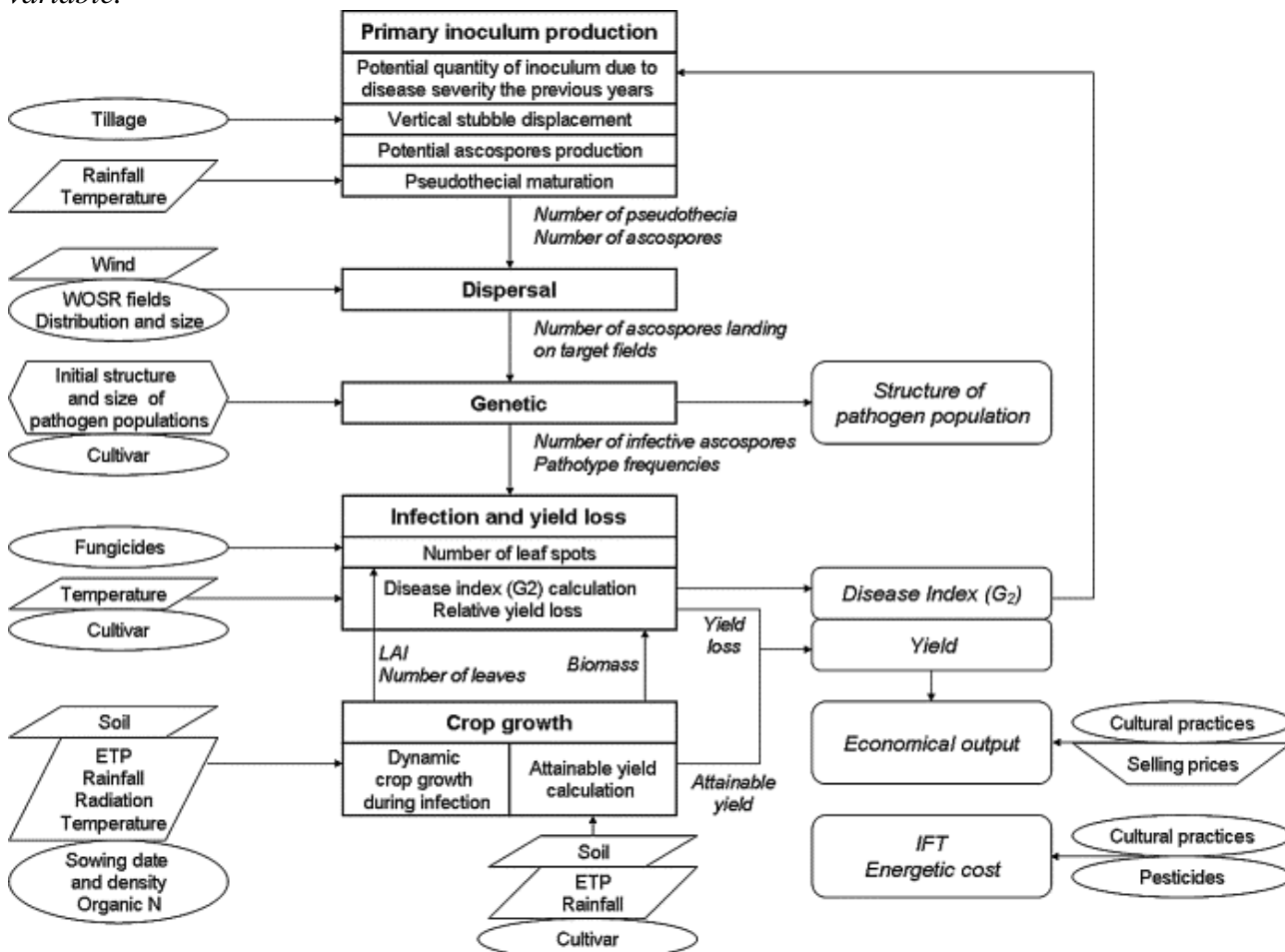
The genetic sub-model takes into account pathotype frequencies in the pathogen population of each oilseed rape field and simulates the ability of pathotypes to infect cultivars with a specific resistance.

Evolutionary forces represented in SIPPOM are migration, selection, and recombination between two or three avirulence genes.

The infection sub-model, derived from Aubertot et al. (2004b), simulates the severity of the disease (*i.e.*, the dynamics of the number of phoma leaf spots per plant and the G_2 severity disease index at crop maturity, Aubertot et al., 2004c) as a function of the number of ascospores that can infect a cultivar (virulent ascospores), the growth-state of the crop, the weather, the fungicide treatment, and the quantitative resistance of the cultivar. It also simulates yield losses.

Input variables of SIPPOM fall into one of four categories: agronomical (description of cultural practices, including the cultivar choice), epidemiological (description of the quantity of initial primary inoculum), genetic (structure and size of the pathogen population), and environmental (description of soil and weather characteristics). The model allows multi-year and regional simulations in order to cover the dispersal scale, track disease epidemics in the region, and follow the loss in efficiency of the specific resistance. Output variables fall into five categories: epidemiological (disease severity and yield loss), agronomical (yield), economical (gross margin), environmental, and genetic (Fig. 1).

Fig. 1. Flow chart of SIPPOM-WOSR. Sub-models, as well as parts of sub-models for the sensitivity analysis, are represented by squares, weather and soil input data by diamonds, technical input data by ovals, and output data by rounded squares. Output variables of each sub-model (state variables of SIPPOM) are shown in *italics*. The structure of pathogen populations is an input variable (initial structure), as well as an output variable.



2.2. Sensitivity analysis method

Several methods can be used to analyse the sensitivity of a model to variability in parameters. The choice of a method greatly depends on the objective of the sensitivity analysis, the number of parameters to be tested, and the computing time of the model. The simplest method is to vary one input factor at a time, keeping the others fixed (Monod et al., 2006). However, this method does not take into account interactions between the

tested parameters, and would neither be adapted nor feasible for a complex model such as SIPPOM. Another method consists in defining probability distributions of parameters and generating a large number of input factors values (*e.g.*, Monte Carlo random sampling). However, this method requires a large number of simulations that would not be possible in the case of SIPPOM, again because of the computing time required. The sensitivity analysis presented here is based on establishing a few values for each parameter and testing all the combinations of the tested parameters in a complete factorial design. Moreover, this makes it possible to simultaneously evaluate the influence of many factors, and statistical methods such as ANOVA are readily available and make the analysis of data very practical (Monod et al., 2006, Breukers et al., 2007).

This method does however necessitate numerous simulations when the number of tested parameters is high: if the number of parameters is p and the number of tested values per parameter is n , then the number of required simulations is n^p . Thus, due to the high number of parameters in our case, the sensitivity analysis of each sub-model was carried out independently. All parameters were tested, except for the crop growth sub-model, for which some parameters were selected, as for example in Makowski et al. (2006). Three values for each parameter were defined—a nominal value and two boundary values. The nominal value (VN) corresponds to the initial parameterisation of SIPPOM (detailed in L  Pelzer et al., 2010), and the two boundary values were chosen according to the literature, or fixed at $VN \pm 50\%$ when data on their variability were not available (following Colbach et al., 2004). When the number of required simulations was too high, the sensitivity analysis of the corresponding sub-model was divided into several steps (detailed below). In the latter case, non-currently tested parameters were fixed at their nominal value.

The sensitivity of a model to variations in its parameters depends on the values of input variables (Ruget et al., 2002, Monod et al., 2006). The ranking of the crop management strategies provided by SIPPOM has to be steady when parameters are varied. We apply here the expression ‘production situation’ (De Wit and Penning de Vries, 1982) to the combination of all input variables necessary for the analysis of the given sub-model, including weather and soil conditions as well as cultural practices. Contrasting ‘production situations’ were defined and the steadiness of the ranking of these given ‘production situations’ was tested.

2.2.1. Given ‘production situations’ for all sub-models

Two contrasting crop management strategies and two contrasting weather conditions were defined, thus providing four contrasting ‘production situations’. The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1). The intensive crop management targets a high attainable yield (a cultivar with a high yield potential and a high sowing density, with organic nitrogen applied before sowing and one fungicide application during autumn, in addition to simplified tillage). The integrated crop management targets an average attainable yield (a cultivar with an average potential yield and no organic nitrogen supply before sowing) but involves suitable cultural practices to limit the disease (ploughing after the harvest of WOSR, early sowing date, low sowing density, and a cultivar with a quantitative resistance). Weather data, dating from 1986 to 2006 in Grignon (48.9  N, 1.9  E, 130 m elevation, 40 km west of Paris), were analysed and two contrasting years were selected according to their predictable impact on the disease (year 1 and year 2, Table 2). Four critical periods for the disease and yield development were investigated: the period of pseudothecial maturation (from WOSR harvest to the beginning of winter), the period of crop growth during primary infections (from WOSR sowing to the end of winter), the period considered in SIPPOM to calculate the attainable yield (from the end of winter to harvest), and the entire growing period. Year 1 is supposed less favourable to phoma stem canker than year 2 because the cumulated rainfall and the average temperature were lower. In addition, year 1 may lead to lower attainable yields (for the same reasons, and because the water stress was higher than for year 2). Soil conditions were identical for all situations, except for the maximum water storage that was associated with each crop management method: high for the intensive crop management (180 mm) and low for the integrated crop management (60 mm). The beginning and the end of winter, as well as harvest dates (December 1st, February 15th and July 15th, respectively), were identical for all the years and crop management options.

Table 1. Definition of two different crop management plans for winter oilseed rape fields according to their impact on disease severity and yield.

Cultural practice	Intensive crop management	Integrated crop management
Sowing density	60 plants m ⁻²	30 plants m ⁻²
Sowing date	1/09	15/08
Cultivar	High potential yield (0.56 kg m ⁻²) No quantitative resistance	Medium potential yield (0.46 kg m ⁻²) Quantitative resistance
Fungicide	One application	No application
Organic nitrogen	Orgafor (0.01 kg N m ⁻²)	No Organic nitrogen
Tillage	Chisel plough (20/07-20/08; primary inoculum production sub-model) Rotary harrowing (1/10) Sowing (2/10)	Chisel plough (20/07-20/08; primary inoculum production sub-model) Mouldboard ploughing (20/09) Rotary harrowing (1/10) Sowing (2/10)

Table 2 Two contrasting weather series chosen from the 20-year (1986–2006) weather data at Grignon (France), for their impact on disease and yield elaboration.

Period	Variable	Year 1 (dry and cold)	Year 2 (wet and warm)
Cultural cycle from sowing to harvest	Average temperature	8.9°C	10.0°C
	Total rainfall	288 mm	791 mm
	Average daily radiation	1018 J cm ⁻² d ⁻¹	1123 J cm ⁻² d ⁻¹
From sowing to the end of winter	Average Temperature	8.5°C	9.4°C
	Total rainfall	206 mm	403 mm
	Average daily radiation	678 J cm ⁻² d ⁻¹	798 J cm ⁻² d ⁻¹
From the end of winter to harvest	Hydric deficit= Potential evapotranspiration – Rain	346 mm	73 mm
From harvest to the beginning of winter	Cumulative favourable days to pseudothecial maturation ^a	79	97

^a A day was considered as favourable for maturation of pseudothecia of *Leptosphaeria maculans* if the mean temperature was between 2 and 20 °C and if the cumulative rainfall 11 days up to and including that day exceeded 4 mm (Aubertot et al., 2006b).

2.2.2. Sensitivity analysis of each sub-model

2.2.2.1. Crop growth sub-model

Sensitivity analysis of this sub-model was carried out in two steps entailing variations in parameters involved in the simulation of the crop growth during infections (when plants are receptive to spores, in autumn), and the attainable yield. Only input variables related to crop management or weather (described above) were tested. The number of tested ‘production situations’ was therefore four for both parts of this sub-model (Table 3). Not all parameters were tested for the crop growth sub-model as the total number of parameters is high (56). Parameters thought to highly influence crop growth were chosen for the first step of the sensitivity analysis of this sub-model (Table 4). All parameters used for the attainable yield calculation (second step of the sensitivity analysis) were tested (Table 4).

2.2.2.2. Primary inoculum production sub-model

Sensitivity analysis of this sub-model was divided into four steps entailing variations in the parameters involved in the simulation of vertical stubble displacement in soil layers, potential quantity of inoculum due to disease severity the previous year, potential ascospore production, and pseudothecial maturation (Table 3). In addition to crop management and weather situations, the effect of the date of chisel ploughing (tillage operation, Table 1) was analysed for this sub-model, as this variation is supposed to impact ascospore production and release. Three G_2 severity disease index values were also tested ($G_2 = 1$, $G_2 = 4.5$ and $G_2 = 8$). The number of tested production situations was therefore 24 for the primary inoculum production sub-model (Table 3). All the parameters of the primary inoculum production sub-model were tested (Table 4). The sensitivity analyses of two parts of this sub-model (vertical stubble displacement in soil layers, and potential quantity of inoculum due to disease severity the previous year) are presented in Supplementary material.

2.2.2.3. Infection sub-model

The sensitivity analysis of this sub-model was carried out in two steps entailing variations in parameters involved in the calculation of the number of leaf spots and the G_2 severity disease index and relative yield loss

(Table 3). Input variables related to the crop, required for this sub-model (biomass, leaf area index, phenological stage) were fixed, averaged from all simulations of the crop growth sub-model sensitivity analysis. The number of spores landing on each target pixel was fixed. The number of tested ‘production situations’ was therefore four for the two steps of the sensitivity analysis of this sub-model (Table 3). All parameters of the infection sub-model were tested (Table 4). Extreme values were generally fixed at $VN \pm 50\%$ as no data was available in the literature.

Table 3. Numbers of simulations carried out for each sub-model for various input variables and parameters, and the analysed output variables.

Sub-model	Process	Input variables (number)	Number of parameters	Number of simulations	Output variables tested
Crop growth	Crop growth during infections (when plants are receptive to spores, in autumn)	2 crop management plans 2 years	9	$4 \times 3^9 = 78732$	Number of days to reach the 6-leaf stage LAI 6-leaf stage Biomass beginning/end winter Attainable yield
	Attainable yield	2 crop management plans 2 years	7	$4 \times 3^7 = 8748$	Attainable yield
Primary inoculum production	Potential ascospore production	4 crop management plans (2 \times 2 dates of chisel plough) 2 years 3 G_2 disease index values	9	$24 \times 3^9 = 472392$	Cumulative number of pseudothecia Cumulative number of released ascospores
	Pseudothecial maturation	4 crop management plans (2 \times 2 dates of chisel plough) 2 years 3 G_2 disease index value	7	$24 \times 3^7 = 52488$	
Infection and yield loss	Number of leaf spots	2 crop management plans 2 years	9	$4 \times 3^9 = 78732$	Maximum number of leaf spots G_2 disease index Yield loss Actual yield
	Disease index and relative yield loss	2 crop management plans 2 years	8	$4 \times 3^8 = 26244$	G_2 disease index Yield loss Actual yield

2.2.2.4. Genetic and dispersal sub-models

The sensitivity analyses of these sub-models are presented in Supplementary material.

2.2.3. State and output variables tested

Analysed output variables of each sub-model (that are state variables of the overall model) were chosen according to their impact on output variables (Table 3). The receptivity of hosts to spores is affected by the number and area of leaves, whereas the biomass is used in SIPPOM to calculate the G_2 disease index and the attainable yield. As the crop is more susceptible to infection before the 6-leaf stage (Brunin and Lacoste, 1970), the number of days to reach the 6-leaf stage was chosen for the crop growth sub-model, as well as the leaf area at this stage. The crop biomass at the beginning and end of winter as well as the attainable yield were also analysed. The cumulative numbers of pseudothecia produced as well as those of ascospores released every 30 days from harvest to the end of winter (approximately 180 days after harvest) were chosen for the primary inoculum production sub-model. In the case of the infection sub-model, the maximum number of leaf spots per plant during the vegetative stage, the G_2 disease index, yield loss, and actual yield were used.

2.2.4. Statistical analysis

Statistical analyses were carried out using procedures from SAS V8 for Windows (SAS Institute Inc., 1999). In order to study the effect of varying parameter values, an analysis of variance (GLM) was carried out with all the given output variables. Parameters that were used in the calculation of the given output were entered into the analysis of variance. When the coefficient of determination was low (below 0.6), interactions between parameters were added. The proportion of the coefficient of determination explained by each parameter (interaction) was used as the index of sensitivity of outputs to each parameter (interaction). The analysis of variance was done for each production situation.

In order to assess the ability of SIPPOM to properly rank control strategies under different weather conditions, the steadiness of ranking of contrasting production situations was first evaluated. To do so, the

proportion of the parameter combinations leading to the most frequent ranking was assessed, as well as the proportion where one, two or more changes occurred in the ranking. The most frequent ranking was then compared with experts' opinions (three agronomists from the French National Institute for Research in Agronomy, INRA, and the French technical centre for oilseed crops, CETIOM).

3. Results

3.1. Crop growth sub-model

3.1.1. Crop growth during infections

In the analysis of variations in parameters in the equations linked to crop growth during infections, variations in the output variables "attainable yield" and "number of days to reach the 6-leaf stage" were satisfactory (between 0.07 and 0.52 kg m⁻², and 22 and 47 days, respectively), but variations in other output variables were quite high (between 0.025 and 0.1610 kg m⁻² for "biomass at the beginning of winter", 0.024 and 0.2270 kg m⁻² for "biomass at the end of winter", and 0.04 and 0.6 for the leaf area index at 6-leaf stage). The R^2 ranged from 67% to 99.9% depending on the output variable and the given production situation (crop management plan \times weather and soil). V_{absMin} (minimum nitrogen absorption rate; Table 4) was an important parameter, explaining the majority of the coefficient of determination for the output variables "biomass at the beginning of winter" (57–83% of the R^2), "biomass at the end of winter" (55–93% of the R^2), and "attainable yield" (64–85% of the R^2 , Fig. 2). Variations in parameters dff and SF_{Coty} (leaf life duration and cotyledon area at emergence; Table 4) also significantly affected the three above-mentioned output variables. In the case of the calculation of the output variable "number of days to reach the 6-leaf stage", only two parameters are concerned: the phyllochron and the leaf life duration. Variations in phyllochron explained 96–98% of the coefficient of determination depending on the production situation. This parameter also had a great effect on the "leaf area" (LAI) (explaining 43–68% of the R^2), as well as the V_{absMin} and SF_{Coty} parameters. Finally, four parameters appeared to be the most influential on all output variables: V_{absMin} , dff , SF_{Coty} , and phyllochron.

The ranking of weather \times crop management situations for the output variables "biomass at the beginning of winter", "biomass at the end of winter", and "number of days to reach the 6-leaf stage" were not steady (data not shown). Conversely, integrated crop management led to lower "leaf area". This seems logical given the low water storage of soil associated with the integrated crop management and the non-use of organic nitrogen. The warm and wet year also led to lower "leaf area", which is logical when the water storage is low (integrated crop management), but more surprising when the water storage is high (intensive crop management). Finally, the distinction between crop management and years was clear in the case of the "attainable yield" output variable. The ranking of the "attainable yield" was very steady. As expected, the intensive crop management gave greater "attainable yields" than the integrated crop management, while yields were higher in the second year than in the first. The most frequent ranking was (from the lowest to the highest) integrated-year 1, integrated-year 2, Intensive-year 1, and Intensive-year 2. This steady ranking occurred 96% of the time.

Because of the high variation in output variables, and due to the unsteadiness of the ranking of some of the output variables, the parameters identified as more influential could be better estimated. Tribo  Blondel (1988) and Dejoux (1999) showed variability in parameters depending, for example, on the cultivar. The variation in parameters, particularly those used for the calculation of biomass and leaf area index, could be readily analysed more thoroughly in order to improve their estimation. V_{absMin} has not yet been estimated for WOSR, and the implications of this are discussed below.

To sum up, the two main outputs of this sub-model that play an important role in the overall model, the leaf area (determining the receptivity of the crop to ascospores) and the attainable yield, varied as expected.

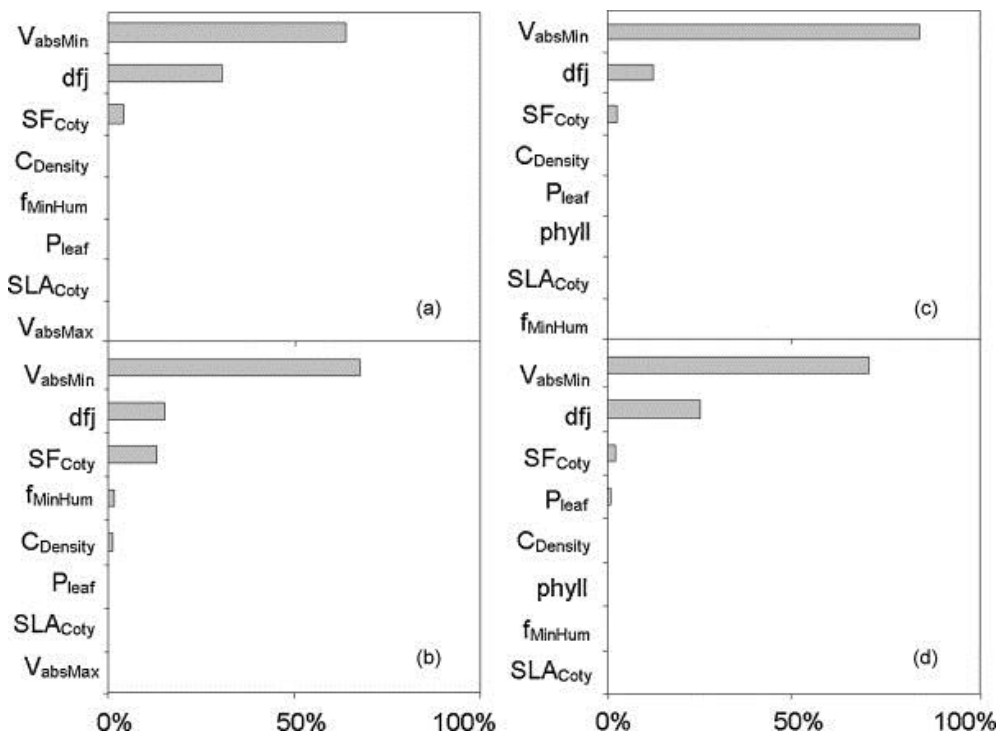
3.1.2. Calculation of the attainable yield

In order to keep realistic values for the attainable yield, the boundary values of parameters of the step 'calculation of the attainable yield' were fixed at $VN \pm 20\%$ instead of $VN \pm 50\%$ (leading to attainable yields varying between 0 and 1.6 kg m⁻²). The effects of parameter values were introduced into the analysis of variance model: R^2 ranged from 89% to 96% depending on the given crop management \times weather situation. The parameter b_{IRdtAtt} used in the calculation of the relative yield loss due to biomass at the end of winter (Table 4) was important as it explained 54–86% of the coefficient of determination R^2 for the "attainable

yield". In this sub-model, this one parameter, in the relationship between attainable yield and biomass, should be more carefully estimated, or the formalism could be changed based on new data.

As concerns the ranking of the "attainable yield", it was stable. Again, as expected, the intensive crop management gave greater "attainable yields" than the integrated crop management, while yields were higher in the second year than in the first. The most frequent ranking was the same as in the first step (occurring 93% of the time).

Fig. 2. Sensitivity analysis of the crop growth calculation during infections (when plants are receptive to spores, in autumn) in the crop growth sub-model. Sensitivity of the output "attainable yield" to parameter variations: percentage of the coefficient of determination explained by each parameter as a function of the simulated situation. (a) Intensive crop management – year 1; (b) intensive crop management – year 2; (c) integrated crop management – year 1; (d) integrated crop management – year 2. The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1): the intensive crop management targets a high attainable yield whereas the integrated crop management targets an average attainable yield but involves suitable cultural practices to limit the disease. The two contrasting years (year 1 and year 2, Table 2) were selected according to their predictable impact on the disease. V_{absMin} : minimum N absorption rate ($\text{kg ha}^{-1}(\text{ C d})^{-1}$), dfj : leaf life duration ( C d), SF_{Coty} : cotyledon area at emergence (m^2), $C_{Density}$: proportion of sown plants that germinate, $phyll$: phyllochron ( C d), SLA_{Coty} : dry biomass at emergence (g m^{-2}), P_{leaf} : proportion (biomass) of leaves in aerial part of plant, V_{absMax} : maximum N absorption rate ($\text{kg ha}^{-1}(\text{ C d})^{-1}$), f_{MinHum} : humus mineralisation ($\text{kg ha}^{-1}(\text{ C d})^{-1}$) (Table 4).

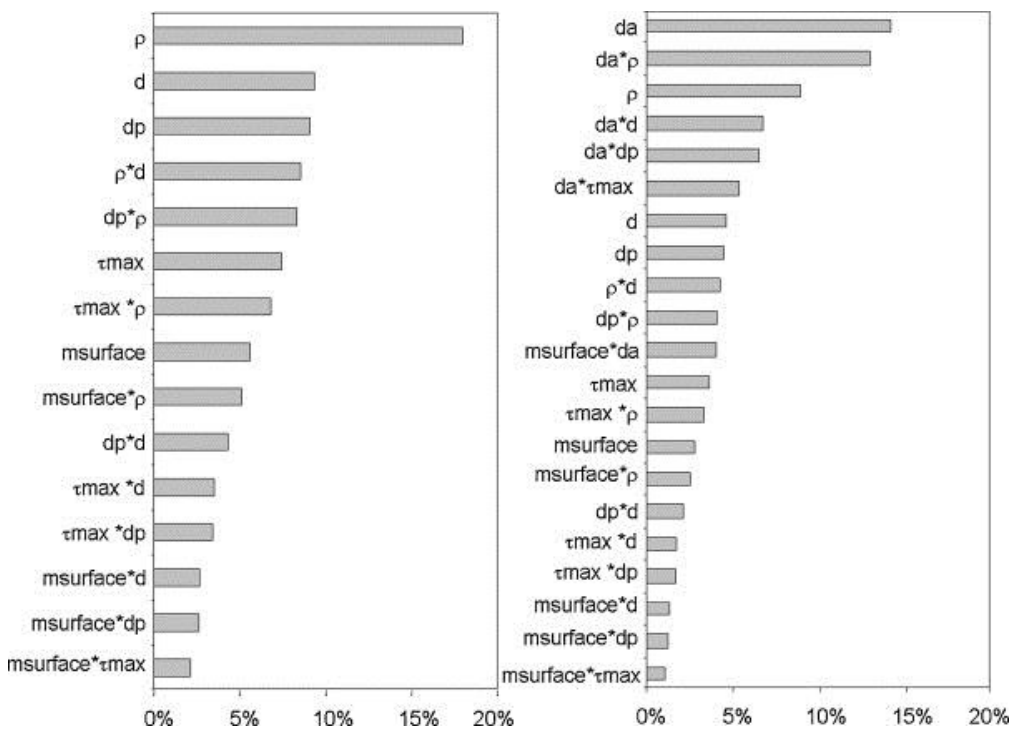


3.2. Primary inoculum production sub-model

In terms of the 'potential ascospore production' step of the sensitivity analysis, output variables highly varied (e.g., from 10^3 to 10^{12} released ascospores 180 days after emergence). Parameters and interactions were introduced into the variance analysis model, and R^2 ranged from 57% to 78% depending on the output variable and the given crop management \times weather \times G_2 severity disease index situation. For the "cumulative number of pseudothecia", the variation in parameter ρ (average bulk density of stubble; Table 4) explained 18% of the coefficients of determination (Fig. 3), whatever the cumulative number of days and the input situation, thereby highlighting the importance of stubble state for inoculum production. Less surprisingly, parameters d (average diameter of stubble, characterizing its size; Table 4) and d_p (maximum density of pseudothecia on 1 m^2 of

stubble; Table 4) and interactions between these three parameters also slightly affected the “cumulative number of pseudothecia”. As concerns the “cumulative number of released ascospores”, the variation in parameter d_a (number of ascospores per pseudothecium; Table 4) explained 13–15% of the coefficients of determination (Fig. 3), whatever the cumulative number of days and the input situation. Parameters ρ , d , d_p (Table 4), and interactions between these parameters and d_a , also significantly influenced the “cumulative number of released ascospores”.

Fig. 3. Sensitivity analysis of the calculation of the potential ascospore production in the primary inoculum production sub-model. Sensitivity of the output variables “cumulative number of pseudothecia over 180 days” (a) ($R^2 = 77\%$) and “cumulative number of released ascospores over 180 days” (b) ($R^2 = 5\%$) to parameter variations, for intensive crop management, early chisel plough, $G_2 = 4.5$, year 1. Results were similar for other simulated situations. Parameters or interactions that are not presented explained less than 1% of the coefficient of determination. The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1): the intensive crop management targets a high attainable yield whereas the integrated crop management targets an average attainable yield but involves suitable cultural practices to limit the disease. The two contrasting years (year 1 and year 2, Table 2) were selected according to their predictable impact on the disease. m_{surface} : surface stubble weight after harvest (kg m^{-2}), d_a : number of ascospores per pseudothecia, τ_{max} : maximum recovering rate of stubble by pseudothecia, d_p : maximum density of pseudothecia on stubble (m^{-2}), ρ : average bulk density of stubble (kg m^{-3}), d : average diameter of stubble (m) (Table 4).

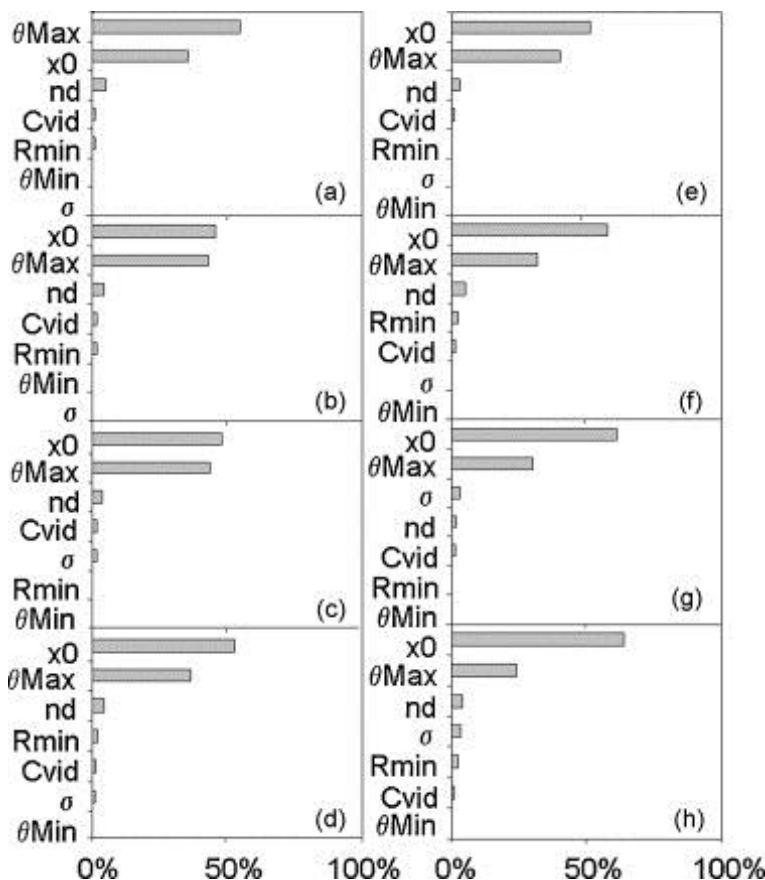


In the ‘pseudothecial maturation’ step, output variables also varied highly (e.g., from 0 to 10^9 released ascospores 180 days after emergence). R^2 ranged from 64% to 85%. The sensitivity analysis showed that the parameters θ_{max} and x_0 (maximum temperature for favourable day and number of favourable days to maturation, Table 4) highly influenced the “cumulative number of pseudothecia” as well as the “cumulative number of released ascospores”, whatever the production situation (Fig. 4).

In terms of the ranking, and whatever the step of the sensitivity analysis of the primary inoculum production sub-model, the average “cumulative number of pseudothecia” and “cumulative number of released ascospores” increased with the initial G_2 severity disease index, whatever the crop management \times weather situation. At a given G_2 severity disease index, integrated crop management led to a much lower “cumulative number of pseudothecia” and “cumulative number of released ascospores”. This was due to mouldboard

ploughing that buries part of the stubble. The later use of chisel ploughing resulted in a small increase in the “cumulative number of pseudothecia” and “cumulative number of released ascospores”. Although the number of days favourable to maturation was higher in year 2 than in year 1, the “cumulative number of pseudothecia” was slightly smaller in year 2. However, the “cumulative number of released ascospores” increased with the number of rainy days (ascospores are released as soon as it rains), and was therefore higher in year 2. The ranking of the output variables “cumulative number of pseudothecia” and “cumulative number of released ascospores” was very stable, particularly the “cumulative number of pseudothecia”, less dependent on weather conditions than the other variables.

Fig. 4. Sensitivity analysis of the calculation of the pseudothecial maturation in the primary inoculum production sub-model. Sensitivity of the output variable “cumulative number of released ascospores over 180 days” to parameter variations for $G_2 = 4.5$, as a function of the simulated situation. (a) Intensive crop management, early chisel ploughing, year 1. (b) Intensive crop management, late chisel ploughing, year 1. (c) Intensive crop management, early chisel ploughing, year 2. (d) Intensive crop management, late chisel ploughing, year 2. (e) Integrated crop management, early chisel ploughing, year 1. (f) Integrated crop management, late chisel ploughing, year 1. (g) Integrated crop management, early chisel ploughing, year 2. (h) Integrated crop management, late chisel ploughing, year 2. The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1): the intensive crop management targets a high attainable yield whereas the integrated crop management targets an average attainable yield but involves suitable cultural practices to limit the disease. The two contrasting years (year 1 and year 2, Table 2) were selected according to their predictable impact on the disease. θ_{max} : maximum temperature ($^{\circ}\text{C}$) for favourable day, θ_{min} : minimum temperature ($^{\circ}\text{C}$) for favourable day, R_{min} : cumulative rain threshold for favourable day (mm), n_d : number of days of cumulative rain, x_0 : number of days favourable to maturation, σ : deviation in number of favourable days, C_{vid} : released ascospore coefficient (mm^{-1}) (Table 4).



Even if the variation in output variables was high, the ranking was very steady for both steps of the sensitivity analysis of this sub-model. Thus, parameters ρ , d , d_p , and d_a for the first part, and θ_{\max} and x_0 for the second part, estimated by Schneider (2005) and Lô-Pelzer et al. (2009b) on the one hand and Salam et al. (2003) and Aubertot et al. (2006b) on the other, can be taken as they stand and go without improvement when the model is used to rank scenarios. However, if the model were to be used for prediction purposes, their estimation could be improved.

The sensitivity analyses of the two other parts of this sub-model (vertical stubble displacement in soil layers, and potential quantity of inoculum due to disease severity the previous year) are presented in Supplementary material.

3.3. Infection sub-model

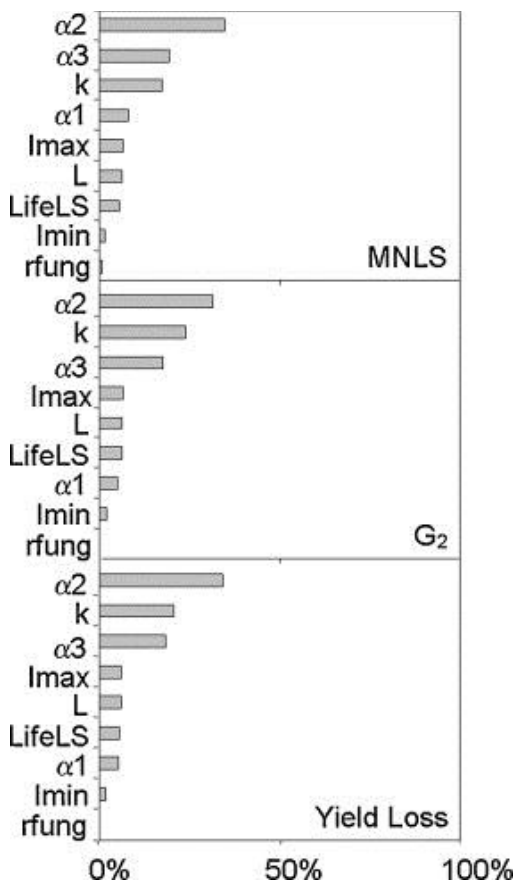
The “maximum number of leaf spots” was variable (between 0 and 670) in the first step of the sensitivity analysis (‘calculation of the number of leaf spots’) whereas the “ G_2 severity disease index”, “yield loss”, and “actual yield” were slightly variable in this step (e.g., the G_2 severity disease index was between 4 and 9). R^2 was 56% for the variation in the output variable “maximum number of leaf spots” and ranged from 75% to 85% for the other output variables (Table 3). Whatever the crop management and weather, variations in parameters α_2 , α_3 (parameters associated to the number of leaves of the host and used in the calculation of the efficiency of infection; Table 4) and k (coefficient of interception of spores, associated with the leaf area; Table 4) had the greatest effect on the “maximum number of phoma leaf spots”, the “ G_2 severity disease index”, and “yield loss” (Fig. 5 for the integrated crop management – year 1).

The “ G_2 severity disease index”, “yield loss”, and “actual yield” were more variable (e.g., G_2 varied between 0 and 9 and yield loss varied between 0 and 80%) in the second step (the ‘ G_2 disease index and relative yield loss’) in comparison with the first step of this sub-model (‘calculation of the number of leaf spots’). R^2 ranged from 66% to 89%. Variations in parameters a_2 and a_0 (parameters used in the G_2 severity disease index calculation; Table 4) had a great effect on “ G_2 severity disease index”, “yield loss”, and “yield” for both crop managements, as well as variations in parameters α_{RQ} (quantitative resistance; Table 4, Fig. 6) for the integrated crop management, whatever the year. Parameter a (used in the relative yield loss calculation; Table 4) also had a great effect on the “yield loss” and “yield” for both crop managements (Fig. 6 for year 1). In the calculation of the G_2 disease index, parameter a_0 is a constant without any biological meaning, whereas parameter a_2 is associated with temperature. It is surprising that these parameter variations had more impact than variations in parameters associated with the number of leaf spots (characterizing the primary infections) or the biomass (characterizing the crop growth), also involved in the calculation of the G_2 disease index. Indeed, weather conditions could overlap with the effect of primary infection and host state, highly dependent on cultural practices. Given this situation, the model could have difficulties to properly simulate differences between crop management.

For the “maximum number of leaf spots”, no clear difference occurred between years, but the number of leaf spots was lower for the intensive crop management, mostly due to the fungicide treatment. Despite this, intensive crop management led to a greater “ G_2 severity disease index” on average and a greater “yield loss”, because of the quantitative resistance of the cultivar used in the integrated crop management. However, as expected, the “actual yield” of the intensive crop management was greater on average as the potential yield of the cultivar was greater (Table 1). As hypothesized, the greater “ G_2 severity disease index” and “yield loss” were associated with year 2, and so was the “yield” (due to a greater attainable yield during this year). The ranking of production situations was stable for both steps. For example, the ranking of production situations for the “yield” output variable in both steps of the sensitivity analysis of this sub-model was (from the lowest to the highest): Integrated-year 1, Intensive-year 1, Integrated-year 2 and Intensive-year 2, meaning again that weather conditions have a higher impact than crop management in this sub-model.

Even if the variation in output variable was high, the rankings were stable for both steps of the sensitivity analysis of this sub-model. Thus, the estimations of parameters identified as more influential (α_2 , α_3 and k , and a_2 , a_0 , and α_{RQ} ; Table 4) can be taken as they stand and go without improvement when the model is used to rank scenarios. However, were the model to be used for prediction purposes, their estimation could be improved. Parameters α_2 , α_3 and k , based on literature (Table 4), would be the most difficult to estimate, as discussed below.

Fig. 5. Sensitivity analysis of the calculation of the number of phoma leaf spots per plant in the infection sub-model. Sensitivity of the maximum number of phoma leaf spots per plant (MNLS), the G_2 disease index and yield loss output variables to parameter variations, for the intensive crop management, year 1 situation ($R^2 = 56\%$; 81% ; 76%). Results were similar for all simulated situations. The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1): the intensive crop management targets a high attainable yield whereas the integrated crop management targets an average attainable yield but involves suitable cultural practices to limit the disease. The two contrasting years (year 1 and year 2, Table 2) were selected according to their predictable impact on the disease. k : coefficient of interception of ascospores, r_{fung} : fungicide persistence (day), I_{max} , I_{min} , α_1 , α_2 , α_3 : parameters used to calculate the efficiency of infection, L : latency (delay in appearance of leaf spot) ($^{\circ}C$ d), $Life_{LS}$: leaf spot duration ($^{\circ}C$ d) (Table 4).



4. Discussion

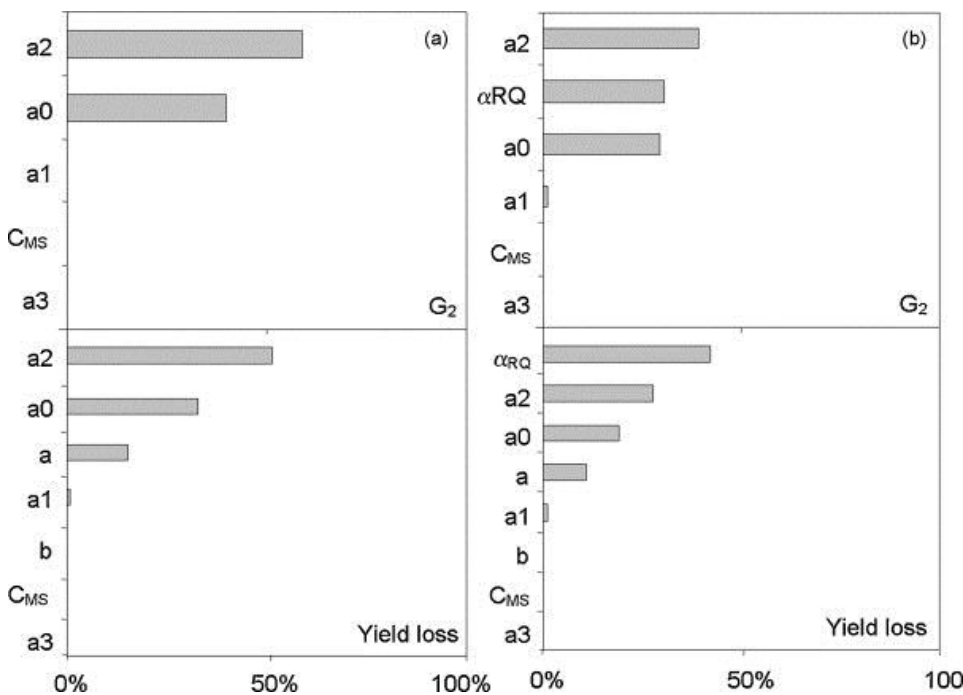
4.1. Sensitivity of output variables to parameter variation: consequences for improvements of the model

Due to the complexity of SIPPOM, in a first approach, the sensitivity analysis was carried out for each sub-model independently. The first aim was to test the sensitivity of state variables (sub-models output variables) to variations in parameters. The variation in output variables was generally high, such that the parameters need to be estimated with a higher precision in order to improve the predictive quality of the overall model. We discuss here some of those parameters that require more experiments or data analysis, as well as necessary improvements of the model revealed by its sensitivity to variations in parameters.

The sensitivity analysis of the crop growth sub-model shows three aspects that need improvement. Firstly, parameter V_{absMin} , characterizing the nitrogen absorption by the crop, had a great impact on outputs, as it explained the majority of the coefficient of determination for output variables such as “biomass at the beginning of winter”. However, this parameter has not yet been estimated for winter oilseed rape: the value for wheat was used in this study (Jeuffroy and Recous, 1999). Sensitivity analysis emphasized therefore the necessity to estimate this parameter for WOSR. Secondly, because of the variability in and unsteadiness of

output variables “biomass” and “number of leaves”, the prediction of these variables needs to be improved. Thirdly, in view of the high variability of the attainable yield when parameters are varied (between 0 and 1.6 kg m^{-2}), it is necessary to carry out more experiments to estimate parameters implied in this part of the model, particularly those involved in the relationship between attainable yield and biomass.

Fig. 6. Sensitivity of the calculation of the disease index and relative yield loss in the infection sub-model. Sensitivity of the G_2 disease index and yield loss output variables to parameters variation, as a function of the simulated situation. (a) Intensive crop management year 1 ($R^2 = 87\%$; 80%). (b) Integrated crop management year 1 ($R^2 = 77\%$; 67%). The two contrasting crop management strategies for WOSR were defined according to the expected impact on both disease severity and attainable yield (Table 1): the intensive crop management targets a high attainable yield whereas the integrated crop management targets an average attainable yield but involves suitable cultural practices to limit the disease. The two contrasting years (year 1 and year 2, Table 2) were selected according to their predictable impact on the disease. C_{MS} : conversion of dry biomass into fresh biomass, a, b: parameters used to calculate the relative yield loss, DI_{max} , a_0 , a_1 , a_2 , a_3 : parameters used to calculate the disease index, α_{RQ} : effect of quantitative resistance (Table 4).



The parameter estimations of the primary inoculum production sub-model were based on joint studies carried out in France, Poland, and Australia (Salam et al., 2003, Aubertot et al., 2006b, Schneider, 2005, Lô-Pelzer et al., 2009a, Lô-Pelzer et al., 2009b). The sensitivity analysis showed that SIPPOM behaved in a consistent way as the ranking of production situations was steady when parameters were varied. Parameter nominal values of this part of the model can therefore be used with confidence. The parameter ρ (density of stubble) highly impacted outputs. Indeed, the effects of rainfall and temperature on pseudothecia production are well documented (e.g., Salam et al., 2003) but less information is available on the impact of the state of the stubble (e.g., density, stubble temperature, and humidity, etc.). The sensitivity analysis highlighted the importance of studying these aspects more precisely in order to improve the predictive quality of the model.

The sensitivity analysis of the infection sub-model highlights three main issues. Firstly, it shows how important the parameters for the calculation of the number of leaf spots are, whereas parameter estimations are only based on data from Brunin and Lacoste (1970) and Biddulph et al. (1999). Secondly, the variation in the parameter linked with weather conditions had more impact on the G_2 disease index than the one linked with the primary infection and crop status, when a greater impact of leaf infection was expected. Thirdly, the parameter representing the effect of quantitative resistance also had a great impact, whereas little data was available for its estimation (Lô-Pelzer et al., 2010). Consequently, the relationship between the number of

spores, crop status (*e.g.*, the number of leaves, leaf area), the number of leaf spots, and subsequent disease severity should be further investigated, but such experiments are not so easy to set up and follow.

4.2. Stability of ranking of production situations when parameters are varied: consequences for the potential use of the model

The second objective of the sensitivity analysis was to assess the steadiness of the rankings of contrasting production situations when parameters are varied. The rankings of input situations were generally stable whatever the parts of the sub-models, although some output variables varied greatly. Moreover, the rankings of input situations were in accordance with experts' opinion. Given the objective of the model, which is to rank sustainable control strategies for phoma stem canker on oilseed rape, these results show that SIPPOM, as it stands, is a satisfactory tool for such use.

As expected, year 2 led to greater attainable yields than year 1 for a given crop management. Intensive crop management caused higher attainable yield for a given year, because the potential yield of the given cultivar and the sowing density were higher, in addition to the fact that organic nitrogen was applied after the harvest of the preceding crop in the case of this crop management.

The quantity of buried stubble was higher in the case of integrated crop management because of the mouldboard ploughing, and the number of released ascospores under this crop management was thus lower, for a given year. Year 2, supposedly more favourable to disease, led to a greater number of released ascospores for a given crop management. Intensive crop management resulted in a smaller number of phoma leaf spots for a given year, mostly due to the fungicide treatment used in this crop management, even if this treatment is not always efficient in fields, depending on the coincidence between the date of application and ascospore showers (Penaud et al., 1999). A lower G_2 disease severity index as well as a smaller yield loss was observed under the integrated crop management because of the quantitative resistance of the cultivar chosen for this crop management (Table 1). However, if cultural control methods such as early sowing or lower crop density are to be investigated, the representation of the quantitative resistance of the given cultivar in SIPPOM would require finer tuning.

Compensations occurred between the effect of weather and crop management on disease and yield. Even if the disease severity and yield loss were less under integrated crop management, the actual yield was also lower because of the lower potential yield of the cultivar, in turn leading to a lower attainable yield. Similarly, year 1, which was less favourable to disease (lower G_2 severity disease index and yield loss), led to a smaller yield because of a smaller attainable yield. While the interactions between the effects of cultural practices and weather conditions are not easily forecasted given the complexity of IPM systems, SIPPOM can be used to assess such interactions.

4.3. Sensitivity analysis method

The method used to conduct the sensitivity analysis was based on a complete factorial design for parameter variation for independent sub-models. This approach has been used, for instance, for the sensitivity analysis of 'GeneSys' (Colbach et al., 2004). With this approach, interactions between input variables and parameter values were accounted for, but interactions between sub-models were not taken into account. It would be necessary to test the sensitivity of the overall model to both input variables and parameter variation, testing thereby the influence of technical, soil, and weather input variables as well as their spatial distribution in the region. However, at this time, the complexity and the computing time of SIPPOM render this undertaking intractable. Methods based on Bayesian statistics (O'Hagan, 2006) are currently being developed. These approaches are based on the development of an emulator that is a statistical approximation of the model (O'Hagan, 2006). They are not yet available for complex models, but could be used later for the sensitivity analysis of the overall model, as they reduce the number of runs needed.

5. Conclusion

A sensitivity analysis of SIPPOM adapted to Phoma stem canker in WOSR was carried out. A complete factorial design was used to test the sensitivity of state variables (sub-model output variables) to variations in parameters, and to test the steadiness of the ranking of contrasting control strategies under various weather conditions when parameters are varied. Contradictions in terms of impact of crop management in interaction

with weather and soil conditions on disease severity and on yield illustrate difficulties in designing integrated cropping systems at a regional scale. It also indicates that simulations should be run under a larger range of weather and soil conditions. However, given the objective of the model, which is to rank IPM strategies to durably bring under control phoma stem canker in the case of oilseed rape, these results show that SIPPOM, as it stands, is a satisfactory tool for such use. Thanks to a sensitivity analysis to input variables (*e.g.*, Breukers et al., 2007, Skelsey et al., 2009), the next step will be to identify strategies that can be implemented to durably control the disease, including combinations of control methods within a single field as well as the spatial distribution of cropping systems within a region.

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Appendix A. Supplementary data

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