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Two weather-based models for predicting the onset of seasonal release of ascospores of *Leptosphaeria maculans* or *L. biglobosa*

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Weather-based models (Improved Blackleg Sporacle and SporacleEzy) to predict the date of onset of seasonal release from oilseed rape debris of ascospores of *Leptosphaeria maculans* or *L. biglobosa*, causes of phoma stem canker, were developed and tested with data from diverse environments in Australia, Canada, France, Poland and the UK. Parameters were estimated, using the same datasets from experiments in the UK and Poland, with an accuracy of root mean squared deviation (*RMSD*) of 7·4 (with a bias of –4·54, *L. maculans*) and 8·5 (with a bias of 0·30, *L. biglobosa*) days for Improved Blackleg Sporacle, and of 2·9 (with a bias of –0·06, *L. maculans*) and 7·3 (with a bias of –1·18, *L. biglobosa*) days for SporacleEzy. When tested with data independent of those used for parameter estimation, overall predictions agreed well with observed data in five countries, both for Improved Blackleg Sporacle (R^2 = 0·96, slope = 1·00, standard error = 0·03, P > 0·05, n = 46) and SporacleEzy (R^2 = 0·96, slope = 0·98, standard error = 0·03, P > 0·05, n = 46). However, SporacleEzy performed better in Australia, Canada, Poland and the UK (*RMSD* = 10·6, 9·7, 5·4 and 3·4 days, respectively) than Improved Blackleg Sporacle (*RMSD* = 11·7, 11·0, 5·6 and 6·5 days, respectively). In contrast, the prediction from Improved Blackleg Sporacle (*RMSD* = 8·0 days) was better in France than that from SporacleEzy (*RMSD* = 15·9 days). Sensitivity analysis showed that better parameter estimation could improve the quality of prediction of SporacleEzy (*RMSD* = 7·6 days) under French conditions. These models are capable of estimating the first seasonal release of ascospores of organisms causing phoma stem canker on oilseed rape under many climates and thus could contribute to development of strategies for control of the disease.

Keywords: blackleg, *Brassica napus*, canola, disease forecasting, phoma stem canker, pseudothecial maturation

Introduction

Phoma stem canker (blackleg), caused by a complex of *Leptosphaeria* species (Mendes-Pereira *et al*., 2003), is a common disease on oilseed rape (canola, *Brassica napus*). Its importance in the main oilseed-rape-growing areas of Australia, Canada, Europe and other countries is well recognized, in terms of its occurrence, spread and diversity (West *et al*., 2001; Howlett, 2004; Fitt *et al*., 2006). Where the disease occurs, usual yield losses at harvest are < 10%, although they can reach 30–50% (West *et al*., 2001). Losses were estimated to be about €56 M per season (for harvest years 2000–02) in the UK, €11·3–30·1 M (for harvest years 1998 and 1999) in Australia and €36·8–147 M (for harvest years 2000–02) in France (Fitt *et al*., 2006). The disease is associated with at least two distinct pathogen species (Williams & Fitt, 1999; Mendes-Pereira *et al*., 2003), *Leptosphaeria maculans*

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and *L. biglobosa* (formerly A-group and B-group of *L. maculans*, respectively). Of the two species, *L. maculans*, associated with damaging stem-base canker in many countries (West *et al*., 2001), is the most important. *Leptosphaeria biglobosa* is mainly associated with upper-stem lesions; while these are usually less severe (Fitt *et al*., 2006), they can still cause serious yield losses in countries like Poland, where summer temperatures are high (Jędryczka *et al*., 1999; Huang *et al*., 2005).

The epidemiology and severity of phoma stem canker differs between continents because of differences in the pathogen population structure, oilseed rape type (spring or winter type) and cultivar grown, climate and agricultural practices (West *et al*., 2001). However, there are similarities in the life cycles of the pathogens. The disease is monocyclic in Australia, Canada and Europe (West *et al*., 2001). Epidemics of phoma stem canker on oilseed rape are largely initiated by airborne ascospores of *Leptosphaeria* species (Bokor *et al*., 1975; McGee, 1977; Hershman & Perkins, 1995; Thürwächter *et al*., 1999; West *et al*., 1999), released from maturing pseudothecia (ascocarps) on the exposed woody remains of the infested stubble (McGee, 1977), predominantly from crops harvested at the end of the previous season. There are differences in the timing of onset of seasonal ascospore release between different countries. For example, ascospores are first released in May in Australia with the start of winter rainfall (Bokor *et al*., 1975; McGee, 1977; Khangura *et al*., 2001), during June in western Canada after a long, cold winter (Kharbanda, 1993) and in late September/early October in western and central Europe at the start of autumn (Gladders & Symonds, 1995; Thürwächter *et al*., 1999; Aubertot *et al*., 2004; Huang *et al*., 2005).

Be it in the autumn (Europe), spring (Canada) or winter (Australia), a recent review (West *et al*., 2001) indicated that the most severe stem-base (crown) cankers, causing substantial yield loss, originate from cotyledon and leaf lesions produced on young plants early in the growing season. However, the relationship between sowing date and severity of phoma stem canker at the end of the crop season is unclear because of variability in the timing of the onset of ascospore release (Aubertot *et al*., 2004). It is therefore important to know the timing of the onset of seasonal ascospore release to guide decisions on phoma stem canker management at regional and farm scales (West *et al*., 1999). The timing of onset of seasonal ascospore release also differs between locations within a country and between seasons at a location (Petrie, 1995; Salam *et al*., 2003; Huang *et al*., 2005). The development of a reliable system for forecasting the onset of ascospore release requires an understanding of this variability (West *et al*., 1999). A scheme to predict the onset of ascospore release would help decision making regarding sowing date and fungicide treatments (to seeds and/or foliage).

The main cause of differences in the timing of the onset of seasonal ascospore release is variation in the timing of pseudothecial maturity (West *et al*., 2001; Salam *et al*., 2003). Pseudothecial maturation, in turn, depends on weather conditions, including temperature and wetness (Gladders & Symonds, 1995; Pérès & Poisson, 1997; West *et al*., 1999). Whereas debris wetness is a prerequisite for progress of pseudothecial maturation, excessive wetness does not necessarily accelerate the process (Petrie, 1994; Pérès *et al*., 1999b). Pseudothecia and mature asci of *L. maculans* can be produced on artificial culture medium at temperatures of 16–25°C (Xu *et al*., 1987) or in a controlled environment at 20°C (Pérès *et al*., 1999a). In western Canada, extremely low winter temperatures (< 0°C) stop the pseudothecial maturation process (Petrie, 1986). In Australia, pseudothecia mature rapidly under natural conditions in autumn, providing sufficient rainfall has occurred (Khangura *et al*., 2001). More recently, Toscano-Underwood *et al*. (2003) studied effects of temperature on the stages of maturation of pseudothecia of *L. maculans* and *L. biglobosa* under both controlled environments and natural conditions.

Effects of environmental factors on maturation of ascospores have been studied in other host-pathogen systems as a basis for development of systems to forecast release of ascospores. For example, a degree-day model for maturation of ascospores of *Venturia inaequalis* (cause of apple scab), originally developed by Gadoury & MacHardy (1982) and adjusted by others, has been in use in many countries for estimating cumulative release of mature ascospores over time (Stensvand *et al*., 2005). However, in this model the starting time of the predictions is the first appearance of mature ascospores (i.e. it does not predict first release of ascospores). Few attempts have made to develop a weather-based system for prediction of onset of seasonal ascospore release. A preliminary forecast in France, based on rain-days, predicts that the first release of *L. maculans* ascospores will occur when 16–19 rain-days have elapsed since harvest and the daily average temperature has decreased to 14°C (Pérès & Poisson, 1997). In Australia, the Blackleg Sporacle forecast, based on temperature and rainfall, predicts that onset of seasonal ascospore release will occur after 43 days have elapsed since harvest, with 10-day average temperature < 22°C and weekly rainfall ≥ 4 mm (Salam *et al*., 2003). However, the application of these forecasts has been limited and they have not been tested outside their countries of origin. This paper reports work to test performance of the Blackleg Sporacle forecast, after re-calibration, for environments in Australia, Canada, France, Poland and the UK, and to describe and test a new improved model (SporacleEzy).

Materials and methods

Definition of 'onset of seasonal ascospore release'

The term 'onset of seasonal ascospore release' is used to designate the date of the first major discharge of *L. maculans* or *L. biglobosa* ascospores from infested oilseed rape debris during a new cropping season. In experiments used for model parameterization or model testing, this date was estimated either by collecting ascospores [e.g. using a Burkard spore sampler (Huang *et al*., 2005)] or by

Table 1 Datasets used for parameterization of the original and Improved Blackleg Sporacle and the SporacleEzy models from experiments to study maturation of *Leptosphaeria maculans* and *L. biglobosa* pseudothecia on oilseed rape debris at Rothamsted under different sets of natural conditions (Toscano-Underwood *et al.*, 2003; Y. J. Huang & B. D. L. Fitt, unpublished) and from experiments to study the pattern of seasonal *L. biglobosa* ascospore release at Poznan, Poland (Huang *et al.*, 2005; M. Jędryczka, unpublished)

Experiment start date	Days to onset of ascospore release	Average daily temperature (°C)[a]	Number of rainfall events (≥ 1·0 mm)[a]
L. maculans, Rothamsted			
04 September 2000	42·8	13·3	26 (18)
28 December 2000	90·3	3·9	59 (39)
30 July 2002	81·9	14·8	25 (16)
12 September 2002	61·3	11·3	28 (20)
25 November 2002	54·0	5·0	39 (25)
L. biglobosa, Rothamsted			
04 September 2000	36·1	14·0	22 (15)
28 December 2000	92·0	4·0	59 (39)
30 July 2002	85·2	14·5	25 (16)
12 September 2002	61·3	11·3	28 (20)
25 November 2002	62·0	5·1	47 (30)
L. biglobosa, Poznan			
18 July 1998[b]	42·8	17·4	34 (23)
18 July 1999[b]	90·3	18·3	39 (21)
18 July 2000[b]	81·9	15·9	29 (18)

[a]For period from start of experiment to onset of ascospore release.
[b]Average date of harvest was used as the start date.

observing the state of pseudothecial maturity on the debris under a microscope on pseudothecia sampled from debris (Toscano-Underwood *et al.*, 2003). In this study, when the measured ascospore data were used, the date of onset of ascospore release was taken as the date when the concentration of ascospores collected was above 10% of the daily maximum (over the measurement period), with the exception of one datapoint which exceeded this range. On the other hand, when the observed state of pseudothecial maturation was used, the date of onset of ascospore release, with few exceptions, was taken as the date when about 50% of pseudothecia were mature (class D, see Toscano-Underwood *et al.* (2003) for definition of pseudothecial maturity classes). Experiments at Rothamsted with infested oilseed rape debris exposed outside showed that the date of onset of ascospore release (Huang *et al.*, 2005) and the date when about 50% of pseudothecia were mature (Huang, 2002) were closely related.

Datasets for estimating model parameters and model testing

Data used for estimating model parameters were from five experiments that measured days until 50% of pseudothecia of *L. maculans* and *L. biglobosa* were mature on oilseed rape debris incubated under natural conditions at Rothamsted, UK, with different starting dates in the period 2000–02 (Toscano-Underwood *et al.*, 2003) and three experiments that measured the onset of seasonal release of ascospores of *L. biglobosa* at Poznan, Poland (Table 1). The exclusive presence of either *L. maculans* or *L. biglobosa* on each piece of debris used in these experiments was confirmed by isolation (West *et al.*, 2002). Weather data [daily average temperature (°C) and daily rainfall (mm)] recorded at Rothamsted and Poznan near the experimental sites were used for operating the models.

Forty-six datasets, 19 from seven locations in Australia, four from two locations in Canada, 10 from six locations in France, four from one location in Poland and nine from two locations in the UK, were used for model testing (Table 2). Each dataset was from an experiment investigating the date of first major ascospore release or date when pseudothecia were mature. Weather data [daily average temperature (°C), daily rainfall (mm)] were from meteorological stations as close as possible (0–3 km) to experimental sites. Weather data for Saskatoon, Saskatchewan, Canada were down-loaded from a website (http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html). Australian weather data were taken from the database of the Department of Agriculture and Food, Western Australia; these weather data, either measured or interpolated, were supplied by the Queensland Department of Natural Resources and Mines (procedure for interpolation described by Jeffrey *et al.*, 2001). French weather data were supplied by the INRA STEFCLI database and by Météo-France. Bimonthly summaries of the air temperature and rainfall data for the location(s) in five countries are presented in Fig. 1. In Australia and Europe, pseudothecial maturity occurs when temperature is decreasing at the start of the growing season; in Canada pseudothecial maturity occurs when temperature is increasing in spring after a long winter with subzero temperatures and snow cover. The average temperatures before the start of the growing season were lower in the UK than at locations in France and Poland. The number of rain events differed considerably between countries; Australia was drier than other countries. There were large differences in numbers of rainfall events between locations within Australia and France, but not between locations in Canada or the UK (not shown).

Blackleg Sporacle model

The pseudothecial maturation module of the Blackleg Sporacle model, developed for Western Australia (Salam *et al.*, 2003), was used. The original module hypothesises that pseudothecial maturation progresses when temperatures are < 22°C and weekly rainfall is ≥ 4 mm (Table 3). Each day after harvest of oilseed rape is classified as either favourable for pseudothecial maturation (*FPM*) or not. A day is designated as *FPM* if the mean daily temperature for the preceding 10-day period is less than a threshold value (*T-threshold*, 22°C) and the total rainfall for the preceding 7-day period is greater than or equal to a threshold (*R-threshold*, 4 mm). A running total (from the beginning of the model run) of *FPM* days is maintained and the date when a specified total of *FPM* days (43) is reached is used

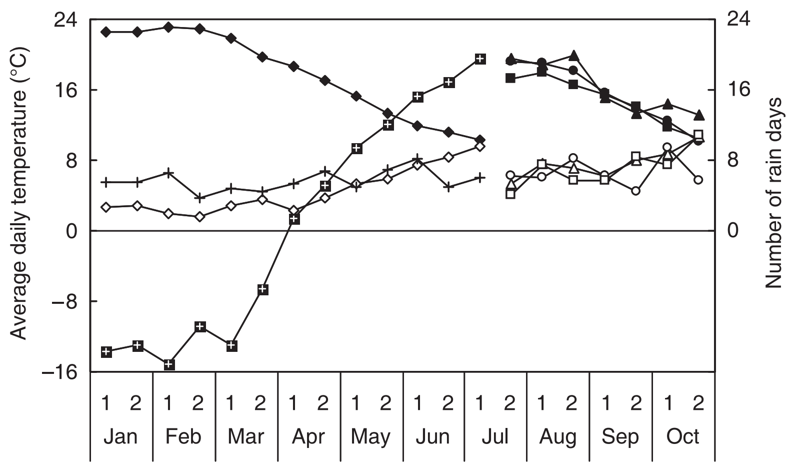

Figure 1 Bimonthly daily air temperature (°C) (◆⊞▲●■) and total number of rain-days (◇+△○□), averaged over location(s) and/or year(s) (see Table 2), in Australia (◆◇), Canada (⊞+), France (▲△), Poland (●○) and the UK (■□) during periods after harvest of oilseed rape (beginning from the start of model simulation, Table 5).

Table 2 Datasets used for testing Improved Blackleg Sporacle and SporacleEzy models from experiments in Australia, Canada, France, Poland and the UK to examine *Leptoshaeria maculans* or *L. biglobosa* pseudothecial maturation or ascospore release under different weather conditions

Country (datapoints)	Location[c]	Observation year	Measurement	Reference
Australia (19)	East Chapman, WA	1998, 1999, 2000	Pseudothecial maturation	Salam *et al.* (2003)
	Merredin, WA	1998, 1999, 2000	Pseudothecial maturation	Salam *et al.* (2003)
	Mount Barker, WA	1998, 1999, 2000, 2002[a], 2004[b]	Pseudothecial maturation	Salam *et al.* (2003) R. K. Khangura & M. J. Barbetti[a] R. K. Khangura[b]
	Wagga Wagga, NSW	2003[a], 2004[a]	Pseudothecial maturation	N. Wratten[a]
	Williams, WA	2003[a]	Pseudothecial maturation	R. K. Khangura & M. J. Barbetti[a]
	Wongan Hills, WA	1998, 1999, 2000, 2002[a], 2004[b]	Pseudothecial maturation	Salam *et al.* (2003) R. K. Khangura & M. J. Barbetti[a] R. K. Khangura[b]
Canada (4)	Carman, Manitoba	2001, 2002	Ascospore release	Guo & Fernando (2005)
	Saskatoon, Saskatchewan	1975, 1976	Ascospore release	McGee & Petrie (1979)
France (10)	Fleury-les-Aubrais	2001[a], 2002[a]	Pseudothecial maturation	J.-N. Aubertot[a]
	Grignon	2000, 2001, 2002[a]	Ascospore release	Aubertot *et al.* (2004) J.-N. Aubertot[a]
	Oizon	2001[a], 2002[a]	Pseudothecial maturation	J.-N. Aubertot[a]
	Rouy	2001[a]	Pseudothecial maturation	J.-N. Aubertot[a]
	Tendu	2002[a]	Pseudothecial maturation	J.-N. Aubertot[a]
	Varennes-les-Narcy	2001[a]	Pseudothecial maturation	J.-N. Aubertot[a]
Poland (4)	Poznan, Wielkopolski region	1998[a], 1999[a], 2000[a], 2001[a]	Pseudothecial maturation	S. Dakowskia & M. Jędryczka[a]
UK (9)	Boxworth	1998, 1999, 2001, 2002	Ascospore release	Huang *et al.* (2005)
	Rothamsted	1998, 1999, 2000, 2001, 2002	Ascospore release	Huang *et al.* (2005)

[a,b]Unpublished.
[c]WA, Western Australia; NSW, New South Wales.

to estimate the date of onset of pseudothecial maturity (*PM-begin*). It has been reported that subzero temperatures can stop the process of pseudothecial maturation in Canada (Petrie, 1986). The original Blackleg Sporacle model does not account for effects of low temperature on pseudothecial maturation, as temperatures in Western Australia between harvest and onset of seasonal ascospore release are never subzero (Salam *et al.*, 2003). Therefore, in the Improved Blackleg Sporacle model a new parameter (*T-lower-threshold*) was incorporated to account for effects on pseudothecial maturation of low temperatures (Table 3), which can occur in many oilseed-rape-growing regions of the world.

SporacleEzy model

The SporacleEzy model is a simplification of the Improved Blackleg Sporacle model (Table 4). The onset of seasonal ascospore release is predicted as the day when the running total of days favourable for pseudothecial maturity (*FPM*) after the oilseed rape harvest reaches *SAR-on*, a model parameter. The *FPM*, a calendar day, is designated as

Table 3 Values of parameters used in the original and Improved Blackleg Sporacle models for predicting date of onset of seasonal *Leptosphaeria maculans* or *L. biglobosa* ascospore release

			Value		
			Original	Improved	
Parameter	Definition	Unit	Western Australia	Australia, Canada, France, UK	Poland
PM-begin	No. days favourable for pseudothecial maturation before onset of ascospore release	days	43	43	50
R-threshold	Lower limit of accumulated rain favourable for pseudothecial maturation	mm	4	4	5
R-threshold-duration	Time period used to calculate *R-threshold*	days	7	7	7
T-threshold-low	Lower limit of mean daily temperature favourable for pseudothecial maturation	°C	–[a]	3	3
T-threshold	Upper limit of mean daily temperature favourable for pseudothecial maturation	°C	22	22	24
T-threshold-duration	Time period used to calculate *T-threshold* and *T-threshold-low*	days	10	10	10

[a]Not included in original version of model.

Table 4 Values of parameters used in the SporacleEzy model for predicting date of onset of seasonal *Leptosphaeria maculans* or *L. biglobosa* ascospore release

			Value	
Parameter	Definition	Unit	Australia, Canada, France, UK	Poland
SAR-on	No. of days favourable for pseudothecial maturation before onset of ascospore release	days	18[a]	18
Rain-threshold	Lower limit of daily rain favourable for pseudothecial maturation	mm	1·0	1·25
T-lower-threshold	Lower limit of mean daily temperature favourable for pseudothecial maturation	°C	6	6
T-upper-threshold	Upper limit of mean daily temperature favourable for pseudothecial maturation	°C	22	24

[a]Sensitivity analysis indicates a value of 14 was better for France.

1 or 0. *FPM* is 1 if daily rain (mm) ≥ *Rain-threshold* and *T-upper-threshold* > average daily temperature (°C) > *T-lower-threshold*.

In addition to *SAR-on*, *Rain-threshold*, *T-lower-threshold* and *T-upper-threshold* are also model parameters. Thus, the SporacleEzy model has four parameters, two less than the Blackleg Sporacle model. The two parameters, *T-threshold-duration* and *R-threshold-duration*, in the Blackleg Sporacle model were eliminated by relating temperature and rainfall functions directly to daily weather conditions.

Start dates for model runs

For the estimation of model parameters, the start dates used were those of the experiments performed outside under natural conditions at Rothamsted, UK (Table 1) or the average date of oilseed rape harvest in Poznan, Poland (Table 5). For model testing, approximated average harvest dates for each country were used (Table 5). Harvest of oilseed rape in Australia occurs during the period October–December, depending on location, and all model runs were started on 1 January, which is after harvest in all areas. The model runs for Canada were also started on 1 January. Although the harvesting of spring oilseed rape is carried out during August in Canada (West *et al*., 2001), temperature rapidly decreases after harvest (averaging around 10, 4, –5 and –15°C in September, October, November and December, respectively) and is soon too low for pseudothecial maturation.

Sensitivity analysis on the parameters for SporacleEzy in relation to onset of seasonal ascospore release

The three estimated parameters (*Rain-threshold*, *SAR-on* and *T-lower-threshold*) were subjected to a sensitivity analysis. This was done to determine the relative importance of these parameters and to ascertain that parameters chosen by parameterization were appropriate for test datasets. The sensitivity analysis was carried out according to a factorial design (Teng *et al*., 1977). Four values of *T-lower-threshold* (–3, 0, 3, 6°C), four values of

Table 5 Oilseed rape sowing time and harvesting time and designated start date of simulation model in five countries for which the original and Improved Blackleg Sporacle and SporacleEzy models were tested

Country	Sowing time	Harvesting time	Start date Julian day (calender day)
Australia	May–June	October–December	1 (1 January)
Canada	Late April to mid-May	Mid-August	1 (1 January)
France	Late August	Mid-July	200 (18/19 July)
Poland	Late August	Mid-July	200 (18/19 July)
UK	Late August	Mid-July	200 (18/19 July)

Rain-threshold (0·5, 1·0, 1·5, 2·0 mm for *L. maculans* and 0·75, 1·25, 1·75, 2·25 mm for *L. biglobosa*) and five values of *SAR-on* (12, 14, 16, 18, 20 days) were tested. These parameter values were chosen around the base parameter set (*SAR-on* 18 days, *T-lower-threshold* 6°C, *Rain-threshold* 1 or 1·25 mm). This range of *T-lower-threshold* and *Rain-threshold* values encompassed laboratory and field observations from around the world (Xu *et al.*, 1987; Petrie, 1994; Pérès & Poisson, 1997; Pérès *et al.*, 1999a; West *et al.*, 2001). The values for *SAR-on* also reflect those reported previously (Petrie, 1986; Rempel & Hall, 1993; Hershman & Perkins, 1995; Pérès *et al.*, 1999a; Toscano-Underwood *et al.*, 2003). The model was run with all combinations of parameters (80 parameter sets) for each datapoint in each country. The weather data used were the data used in the model testing. Model-predicted dates for timing of onset of seasonal ascospore release were compared with observed dates using the root mean squared deviation (*RMSD*) approach.

Statistical analysis

Performance of the model(s), for estimation of parameters and/or testing, was analysed statistically using a correlation-regression approach (predicted value vs. observed value) and/or a deviation approach (predicted value minus observed value) (Kobayashi & Salam, 2000). For the correlation–regression approach, the regression statistics that were used were the coefficient of determination (R^2) for the 1:1 ($y = x$) line and the slope (m) of the regression line which was forced through the origin (Asseng *et al.*, 2000). The standard error of the slope, the level of significance (P) to test whether the slope was different from 1, and the number of points (n) included in the regression analysis were also used.

For the deviation approach, two deviation statistics were used. The mean squared deviation (*MSD*) has three components: squared bias (*SB*), squared difference between predicted and observed standard deviations (*SDSD*) and lack of positive correlation weighted by the standard deviations of predicted and observed values (*LCS*). *MSD* measures the total deviation between predicted and observed values. The lower the value of *MSD*, the closer the predicted value is to the observed value. *SB* indicates the agreement between the predicted and observed means, whereas *SDSD* and *LCS* together show how closely the model predicts variability around the mean. The two sources of this variability are the magnitude of fluctuations among the n observations and pattern of the fluctuations across n observations; *SDSD* and *LCS* quantify the ability of the model to describe the magnitude and pattern of fluctuation, respectively. The other deviation statistic was *RMSD*, the average product of deviations for each datapoint pair in two datasets (Kobayashi & Salam, 2000).

To test model predictions against observed seasonal variability at a location, six locations were selected. They were Mount Barker and Wongan Hills (Western Australia; data for five seasons), Grignon (France; data for three seasons), Poznan (Poland; data for four seasons), Boxworth and Rothamsted (UK; data for four and five seasons, respectively).

Results

Parameter estimation for Improved Blackleg Sporacle model

The residuals of days to onset of seasonal ascospore release of *L. maculans* or *L. biglobosa* predicted by the original and Improved Blackleg Sporacle models were plotted against the observed data (Fig. 2). The *RMSD* between predicted values from the original Blackleg Sporacle model and the observed values was 13·3 days for *L. maculans* and 16·6 days for *L. biglobosa*. These differences were expected since the model did not take into account effects on pseudothecial maturity of low temperature, which might have occurred in some of the experiments (Table 1). The model was run to estimate the effects of five low temperatures (0, 1, 2, 3 and 4°C) on maturation of *L. maculans* pseudothecia; of these temperatures, 3°C, the estimated parameter value, produced the lowest *RMSD* (7·4 days) and a bias of –4·54 days (Fig. 2a).

The parameter set used for *L. maculans* was initially tested for predicting days to onset of seasonal ascospore release by *L. biglobosa*; this showed a *RMSD* of 13·8 days and a bias of 4·58 days between predicted and observed values. The results indicated that the model needed different parameter values for *L. biglobosa*. The re-estimated parameter values, using the SOLVER function of Microsoft® Excel 2002 and listed in Table 3, appeared to be more suitable for *L. biglobosa*, with a *RMSD* of 8·5 days and a bias of –0·30 days between predicted and observed values (Fig. 2b). The SOLVER function of Microsoft® Excel 2002 is designed to define an optimal value for a formula including a number of parameters. In this case, the SOLVER function was used to minimize the *MSD* between observed and simulated values.

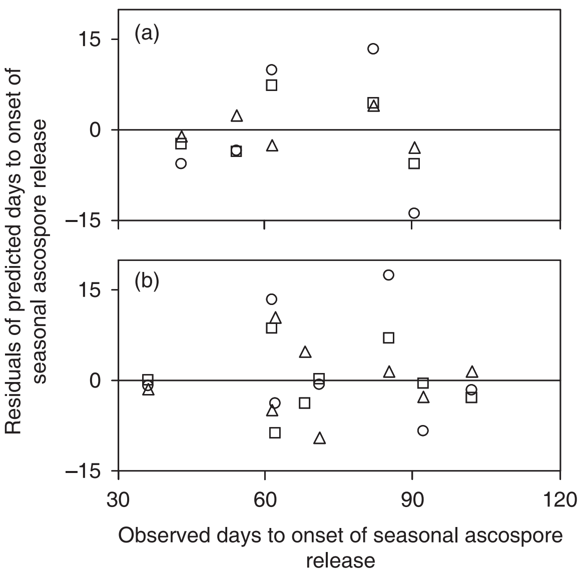

Figure 2 Residuals (observations minus predictions) of days to the onset of release of ascospores of *Leptosphaeria maculans* (a) or *L. biglobosa* (b) predicted by original Blackleg Sporacle (○), Improved Blackleg Sporacle (□) or SporacleEzy (Δ) models plotted against observed values for datasets from experiments at Rothamsted and Poznan (Table 1). (a) *L. maculans* (original Blackleg Sporacle model: root mean squared deviation (*RMSD*) = 13·3 days; bias = –0·54 days; Improved Blackleg Sporacle model: *RMSD* = 7·4 days; bias = –4·54 days; SporacleEzy model: *RMSD* = 2·9 days; bias = 0·06 days). (b) *L. biglobosa* (original Blackleg Sporacle model: *RMSD* = 16·6 days; bias = 7·08 days); Improved Blackleg Sporacle model: *RMSD* = 8·5 days; bias = –0·30 days; SporacleEzy model: *RMSD* = 7·3 days; bias = –1·18 days). Parameter values are listed for original and Improved Blackleg Sporacle models in Table 3 and for SporacleEzy model in Table 4.

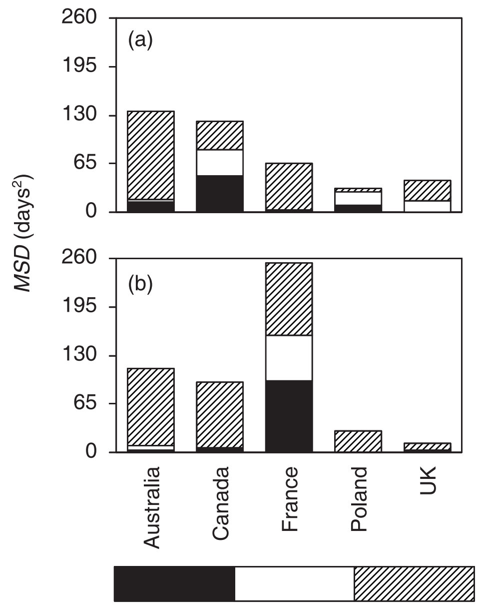

Figure 3 Mean squared deviation (*MSD*) and its components, squared bias (*SB*), squared difference between standard deviations (*SDSD*) and lack of correlation weighted by the standard deviations (*LCS*), comparing predicted and observed dates of onset of seasonal ascospore release in Australia, Canada, France and the UK (*Leptosphaeria maculans*) and Poland (*L. biglobosa*). (a) Predictions from the Improved Blackleg Sporacle model. The parameter values used were the same for all countries except Poland (Table 3). (b) Predictions from the SporacleEzy model (parameters listed in Table 4).

Parameter estimation for SporacleEzy model

In Europe, pseudothecia of pathogens causing phoma stem canker can mature on oilseed rape debris in 2–3 weeks before the onset of seasonal ascospore release, depending on weather conditions (Pérès & Poisson, 1997; Toscano-Underwood *et al*., 2003). Taking this as a guideline, the SporacleEzy model was run for *L. maculans* using a combination of seven low temperatures, *T-lower-threshold* (0–6°C, with 1°C increments) and 17 days (14–30 calendar days, with 1°C increments) favourable for pseudothecial maturation after crop harvest before the onset of seasonal ascospore release (*SAR-on*) with two rainfall thresholds (*Rain-threshold*, 0·6 and 1·0 mm rain per day). The 0·6-mm-rain-per-day threshold was equivalent to the *R-threshold* parameter of the Blackleg Sporacle model (4 mm rain per week); the 1-mm-rain-per-day threshold was an arbitrary figure. The upper temperature threshold (22°C, *T-upper-threshold*) was not changed (*T-upper-threshold*), since during experimental periods there were no days with daily average temperature above the threshold. Among the 238 combinations of parameters, the model parameter values for *L. maculans* were estimated as the set (*SAR-on* 18 days, *T-lower-threshold* 6°C and *Rain-threshold* 1 mm) that produced the lowest *RMSD* (2·9 days) (Fig. 2a).

The parameter values estimated for *L. maculans* were initially tested to estimate parameter values for *L. biglobosa*; this showed a *RMSD* of 8·7 days and a bias of 2·2 days between predicted and observed values. To further improve predictions, parameter values were re-estimated, using the SOLVER function of Microsoft® Excel 2002. The re-estimated values (Table 4) appeared to be more suitable for *L. biglobosa*, giving a *RMSD* of 7·3 days and a bias of –1·18 days between predicted and observed values (Fig. 2b).

Performance of Improved Blackleg Sporacle model

The Improved Blackleg Sporacle model predicted well the onset of seasonal ascospore release in Australia, Canada, France, Poland and the UK. The *RMSD* between observed and predicted dates ranged from 11·7 (Australia) to 5·6 days (Poland) (Fig. 3a). A regression of predicted against observed dates accounted for 96% of the variance ($R^2 = 0·96$, slope = 1·00, standard error = 0·03, $P > 0·05$, $n = 46$) (Fig. 4a). The predicted dates were within 7 days of observed dates for 42, 50, 70, 75 and 78% and within 14 days of the observed dates for 68, 75, 90, 100 and

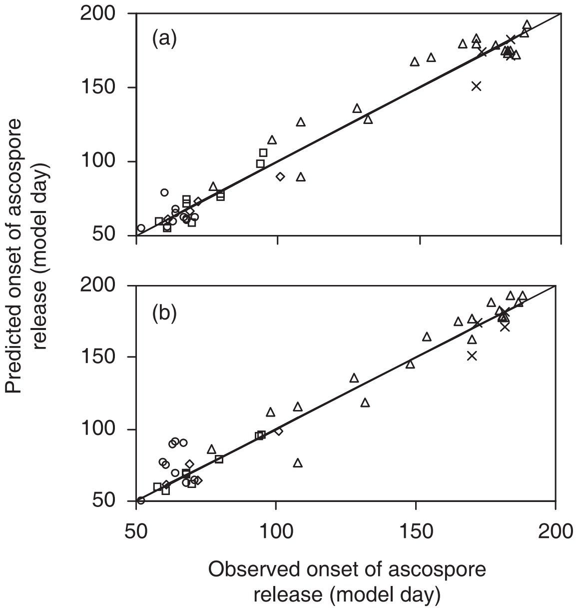

Figure 4 Comparison of observed and predicted time ('model day' – number of calendar days from the start date of model run; Table 5) of onset of seasonal ascospore release in Australia (Δ), Canada (▲), France (○) and the UK (□) (*Leptosphaeria maculans*) and Poland (◇) (*L. biglobosa*). (a) Predictions from Improved Blackleg Sporacle model using parameters in Table 3. The 1:1 line shows no significant difference ($P > 0{\cdot}05$) between predicted and observed values ($R^2 = 0{\cdot}96$, $n = 46$). (b) Predictions for SporacleEzy model using parameters in Table 4. The 1:1 line shows no significant difference ($P > 0{\cdot}05$) between predicted and observed values ($R^2 = 0{\cdot}96$, $n = 46$).

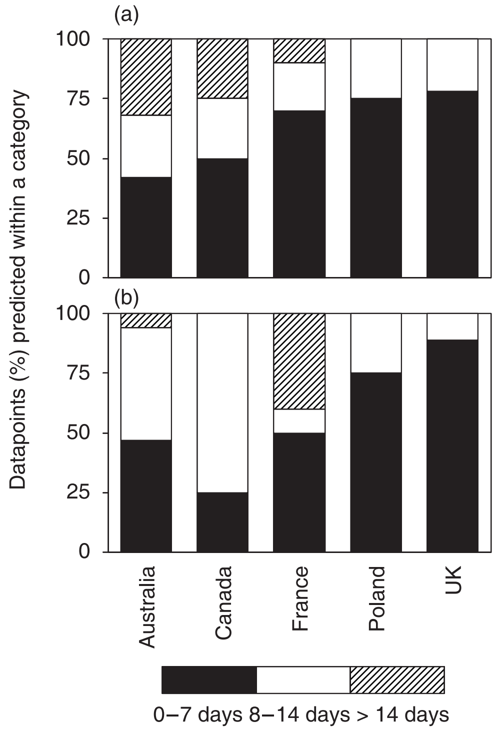

Figure 5 Differences between predicted and observed dates of onset of seasonal ascospore release in Australia, Canada, France, the UK (*Leptosphaeria maculans*) and Poland (*L. biglobosa*). (a) Predictions from Improved Blackleg Sporacle model using parameters in Table 3. (b) Predictions from SporacleEzy model using parameters in Table 4.

100% of the data-points for Australia, Canada, France, Poland and the UK, respectively (Fig. 5a). The model accurately predicted seasonal variability at Grignon (France; *RMSD* = 2·9 days), Rothamsted (UK; *RMSD* = 4·6 days) and Poznan (Poland; *RMSD* = 5·6 days) (Fig. 6a). The prediction was reasonably good for Boxworth (UK; *RMSD* = 8·3 days); for this location differences between standard deviations (expressed as *SDSD*) were the major cause of variability, indicating that the magnitude of seasonal variability was less accurately predicted. For Mount Barker and Wongan Hills (Western Australia), larger differences were observed (*RMSD* = 14·3 and 11·8 days, respectively), associated with poor correlation (expressed as *LCS*) and large *SDSD*, respectively. The poor correlation indicated that the model did not adequately simulate the pattern of seasonal variability.

Performance of SporacleEzy model

The observed dates of onset of seasonal ascospore release in Australia, Canada, Poland and the UK were predicted well by SporacleEzy, with *RMSD* values of 10·6, 9·7, 5·4 and 3·4 days, respectively (Fig. 3b). There was a larger discrepancy between predicted and observed dates with French datasets (*RMSD* = 15·9 days). A regression of predicted against observed dates accounted for more than 96% of the variance ($R^2 = 0{\cdot}96$, slope = 0·98, standard error = 0·03, $P > 0{\cdot}05$, $n = 46$) (Fig. 4b). The predicted dates were within 7 days of the observed dates for 47, 25, 50, 75 and 89% and within 14 days of the observed dates for 94, 100, 60, 100 and 100% of the datapoints for Australia, Canada, France, Poland and the UK, respectively (Fig. 5b). Overall, compared to the Improved Blackleg Sporacle model, the performance of SporacleEzy was slightly better in Australia, Canada, Poland and the UK, but slightly worse in France.

The model very accurately predicted seasonal variability at Rothamsted (UK; *RMSD* = 2·1 days), Boxworth (UK; *RMSD* = 4·6 days) and Poznan (Poland; *RMSD* = 5·4 days) (Fig. 6b). The prediction was reasonably good for Wongan Hills (Western Australia; *RMSD* = 7·3 days). For Mount Barker (Western Australia), a larger discrepancy was observed (*RMSD* = 17·2 days), mainly resulting from poor correlation (expressed as *LCS*). The model did not adequately predict Grignon (France) data-points (*RMSD* = 15·9 days); the differences between the predicted and observed dates were attributed to bias (expressed as *SB*) and *SDSD*. Thus, at Grignon, the model failed to simulate the differences between the means and the size of seasonal fluctuations.

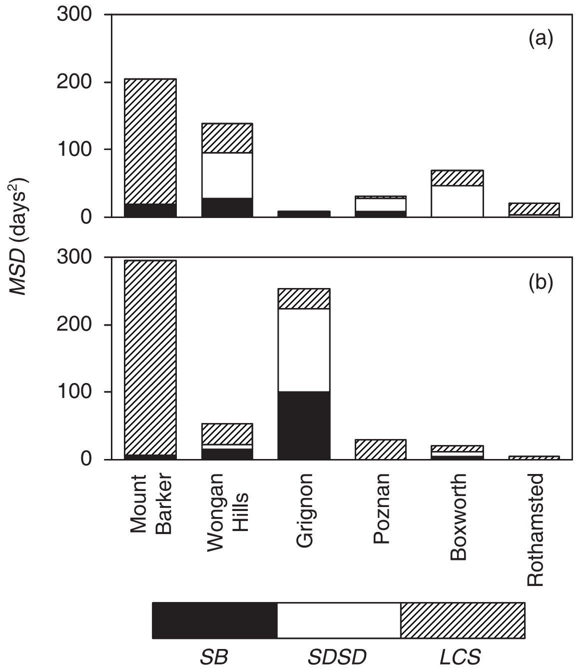

Figure 6 Mean squared deviation (*MSD*) and its components, squared bias (*SB*), squared difference between standard deviations (*SDSD*) and lack of correlation weighted by the standard deviations (*LCS*), comparing dates predicted by models and observed dates for onset of seasonal ascospore release in selected locations in Australia (Mount Barker and Wongan Hills, data for five seasons), France (Grignon, three seasons), UK (Boxworth, four seasons, and Rothamsted, five seasons) (*Leptosphaeria maculans*) and Poland (Poznan, four seasons) (*L. biglobosa*). (a) Predictions from Improved Blackleg Sporacle model used parameters in Table 3. (b) Predictions from SporacleEzy model used parameters in Table 4.

Parameter sensitivity of SporacleEzy model in relation to onset of seasonal ascospore release

The sensitivity of the three parameters, *Rain-threshold*, *SAR-on* and *T-lower-threshold*, in relation to onset of seasonal ascospore release was investigated (Figs 5, 7 and 8). Results, expressed in terms of *RMSD* from observation, indicated that parameter sensitivity was different in Canada from Australia, France, Poland and the UK. Except for Canada, the low temperature threshold (*T-lower-threshold*), in the range of −3 – 6°C, was insensitive, and days to onset of seasonal ascospore release (*SAR-on*) was sensitive in all the countries. The sensitivity of rainfall threshold (*Rain-threshold*) was evident in all the countries, but appeared to have strong interactions with *SAR-on* in Australia, France, Poland and the UK, whereas in Canada its interaction was strong with *T-lower-threshold*, but not *SAR-on*. In Australia, a combination of *SAR-on* 18 days and *Rain-threshold* 1·0 mm as estimated model parameters appeared to be the best (lowest *RMSD*) choice; however, this differed little from a number of other parameter sets [20 days and 0·5 mm; 16 days and 1·0 mm; 18 days and 0·5 mm (*SAR-on* and *Rain-threshold*, respectively)]. In France, with *Rain-threshold* 1·0 mm and *SAR-on* 14 days (note, the model parameter was 18 days) produced the best performance and was distinctly different from other parameter sets. In Poland, the combination of *SAR-on* 18 days and *R-threshold* 1·25 mm (as model parameters) produced the best performance and was distinctly different from other parameter sets. In the UK, as in Australia, the best parameter set was the combination of *SAR-on* 18 days and *R-threshold* 1·0 mm as estimated model parameters; however, this differed little from several other parameter sets [20 days and 1·0 mm; 18 days and 1·5 mm; 16 days and 1·5 mm; 20 days and 0·5 mm (*SAR-on* and *R-threshold*, respectively)]. In Canada, a number of combinations [20 days, 0·5 mm, 6°C; 20 days, 1·5 mm, 0°C; 20 days, 1·5 mm, −3°C; 18 days, 1·0 mm, 6°C; 18 days, 1·5 mm, 0°C; 18 days, 1·5 mm, −3°C; 16 days, 1·0 mm, 6°C; 16 days, 1·5 mm, 6°C; 14 days, 1·5 mm, 6°C (*SAR-on*, *Rain-threshold* and *T-lower-threshold*, respectively)] gave similar or better performances than other combinations.

Discussion

These results show that the date of onset of ascospore release of *L. maculans* or *L. biglobosa* in many different climates across the world can be predicted using a weather-based predictive model with a set of parameters adapted to different cropping and environmental conditions. Of the two models used in this study, the Improved Blackleg Sporacle, introducing effects of low temperature on pseudothecial maturity into Blackleg Sporacle, performed reasonably well when tested with independent data from Australia, Canada, France, Poland and the UK. However, the parameter values for *L. maculans*, the predominant species in Australia, Canada and Western Europe, differed from those for *L. biglobosa*, the predominant species in Poland. To satisfactorily simulate maturation of *L. biglobosa*, parameter values with a higher daily temperature upper threshold, wetter days (i.e. higher rainfall threshold) and more (favourable) days from crop harvest to onset of seasonal ascospore release were required. Toscano-Underwood *et al.* (2003) found that progress of pseudothecial maturation was similar for *L. maculans* and *L. biglobosa* at 15–20°C, but there is little information available about this relationship for higher temperatures.

A new model, SporacleEzy, performed better than the Improved Blackleg Sporacle model in Australia, Canada, Poland and the UK, with more accurate prediction of the date of onset of release of *L. maculans* or *L. biglobosa* ascospores. This model was developed using a simpler approach than that of Blackleg Sporacle and two parameters from the original (and Improved) Blackleg Sporacle model were found to be inadequately defined. They were *R-threshold-duration* (i.e. preceding period of 7 days used in calculating the *R-threshold* value; see Table 3) and *T-threshold-duration* (i.e. preceding period of 10 days used in calculating values of *T-threshold* and *T-lower-threshold*). Furthermore, although the parameter value 43 days favourable for pseudothecial maturation (*PM-begin*) before onset of ascospore release worked well in testing of this

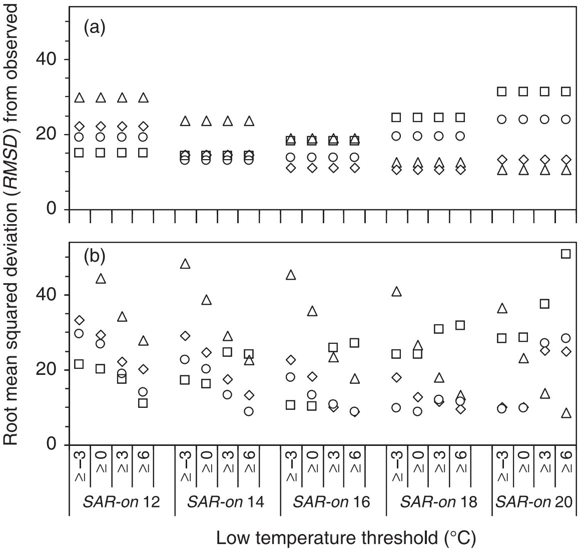

Figure 7 Sensitivity analysis on three parameters in the SporacleEzy model: lower limit of accumulated rain favourable for pseudothecial maturation (*Rain-threshold*), lower limit of mean daily temperature favourable for pseudothecial maturation (*T-lower-threshold*) and total days favourable for pseudothecial maturity after oilseed rape harvest (*SAR-on*) in relation to onset of seasonal ascospore release. Results expressed in terms of root mean squared deviation (*RMSD*) from observed values for the combinations of five values of *SAR-on* (12, 14, 16, 18, 20 days), four values of *T-lower-threshold* (–3, 0, 3, 6°C) and four values of *Rain-threshold* [low (0·5 mm for *L. maculans* and 0·75 mm for *L. biglobosa*), Δ; low+0·5 mm, ◇; low+1·0 mm,○; low+1·5 mm, □]. (a) Australia, (b) Canada.

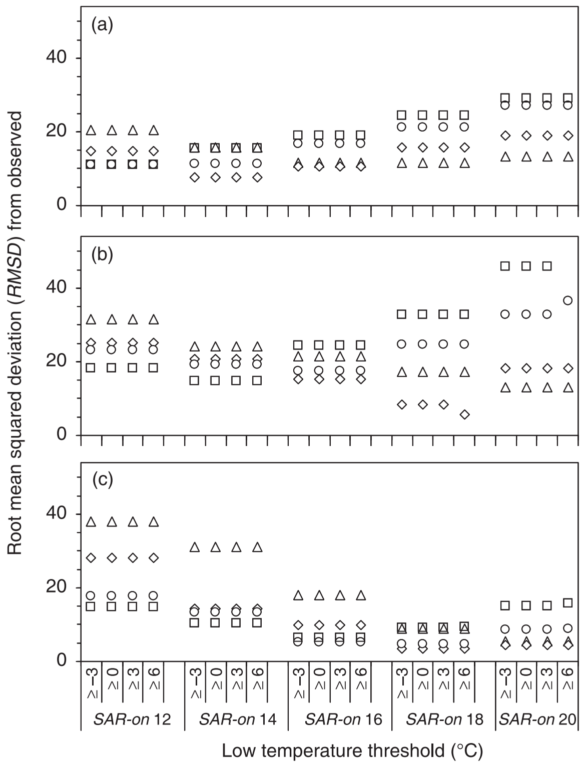

Figure 8 Sensitivity analysis on three parameters in the SporacleEzy model: lower limit of accumulated rain favourable for pseudothecial maturation (*Rain-threshold*), lower limit of mean daily temperature favourable for pseudothecial maturation (*T-lower-threshold*) and total days favourable for pseudothecial maturity after oilseed rape harvest (*SAR-on*) in relation to onset of seasonal ascospore release. Results expressed in terms of root mean squared deviation (*RMSD*) from observed values for the combinations of five values of *SAR-on* (12, 14, 16, 18, 20 days), four values of *T-lower-threshold* (–3, 0, 3, 6°C) and four values of *Rain-threshold* [low (0·5 mm for *L. maculans* and 0·75 mm for *L. biglobosa*), Δ; low+0·5 mm, ◇; low+1·0 mm, ○; low+1·5 mm, □]. (a) France, (b) Poland, (c) UK.

model, it may not apply in all situations. For example, mature pseudothecia can be produced within 2–3 weeks on naturally infested oilseed rape debris at 15–20°C under continuous wetness (Toscano-Underwood *et al*., 2003).

The sensitivity analysis indicated that different combinations of parameter values may need to be applied for different countries. For example, it suggested that a different estimate of *SAR-on* (14 days instead of 18 days) (Table 4) could greatly improve the predictions of SporacleEzy (*RMSD* = 7·6 days vs. test performance of 15·9 days) in France. It is difficult to understand why a different value for *SAR-on* should apply in France to the other four countries. The number of days from crop harvest required for onset of release of ascospores (*SAR-on*) depends on how a day is defined as favourable for pseudothecial maturation in relation to temperature and wetness factors. Two of the three SporacleEzy parameters subjected to sensitivity analysis, rainfall threshold (*R-threshold*) and the number of days to onset of seasonal ascospore release (*SAR-on*), were sensitive in all countries. By contrast, the low temperature threshold (*T-lower-threshold*), below which the pseudothecial maturation process is assumed to stop, was insensitive in Australia, France, the UK and Poland, but sensitive in Canada, where very low winter temperatures occur. The sensitivity analysis also showed that 1·0–1·5 mm of daily rainfall (with appropriate combinations of *SAR-on* and *T-lower-threshold*) was a good estimate of the rainfall threshold for pseudothecial maturation. Wetness is essential for maturation of *L. maculans* and *L. biglobosa* pseudothecia on oilseed rape debris (Toscano-Underwood *et al*., 2003). It has been reported, however, that excessive rainfall is not necessary for maturation to progress (Petrie, 1994; Pérès *et al*., 1999b) and 1·0–1·5 mm of daily rainfall is probably sufficient to allow the oilseed rape stem debris to remain thoroughly wetted.

The insensitivity of the low temperature threshold suggests that, even if there were large errors in estimating this parameter, the accuracy of model predictions would not be affected in Australia, France, the UK and Poland. A threshold of 6°C, the estimated parameter value, may appear too high since there is evidence from controlled-environment experiments that pseudothecial maturation can occur at a constant temperature of 5°C (Toscano-Underwood *et al*., 2003). Two of the experiments used for parameter estimation had an average temperature below

6°C during the whole pseudothecial maturation process; however, the model predictions were still quite accurate in those experiments. In western Canada, where temperature is extremely low for about 6 months soon after oilseed rape harvest, and where this parameter was very sensitive, the estimated value (6°C) appeared to be correct if an appropriate value of daily rainfall threshold was assigned. However, with suitable values of two other parameters, low temperature thresholds of −3°C and 0°C may also be applied to Canadian datasets. This indicates that more information is needed to estimate appropriate values to account for low-temperature effects on pseudothecial maturation in countries like Canada.

This work identifies some important issues in relation to further understanding of phoma stem canker epidemics on oilseed rape. For example, it is still not clear at what extreme temperatures (both low and high) the pseudothecial maturation process stops on oilseed rape debris or whether these temperature extremes differ between *L. maculans* and *L. biglobosa*. Aspects of effects of rainfall (e.g. intermittent rainfall) on the process of pseudothecial maturation on oilseed rape debris also warrant further investigation. Findings on these issues will help increase accuracy of predictions of first release of ascospores of these *Leptosphaeria* species.

This study suggests that the Improved Blackleg Sporacle and SporacleEzy models, predicting onset of ascospore release, can help to improve strategies for management of phoma stem canker in oilseed rape in all five countries. These strategies include altering sowing date (provided weather and farm-work schedules permit sowing) and chemical protection (seed treatment and/or foliar spray treatment) according to the risk of ascospore release during the period when oilseed rape is most susceptible. The Blackleg Sporacle model is already being used in Western Australia to forecast the timing of onset of release of ascospores, a month ahead of the normal sowing time, to guide decisions on sowing dates and/or use of chemicals as seed treatments. SPEC, a program that monitors both pseudothecial maturation and ascospore release in Poland (Jędryczka *et al.*, 2004) will provide data specific to *L. biglobosa* that can be used to improve forecasting systems there. In the UK ascospore release and occurrence of phoma leaf spotting is being used to guide commercial decisions about timing of foliar and fungicide sprays. The new SporacleEzy model can be used to improve current forecasting systems. These models could also be used as templates for models to estimate first release of ascospores of other crop pathogens, such as *Didymella rabiei* and *Mycosphaerella pinodes*, the causal agents of ascochyta blights in chickpea and field pea, respectively.

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