

Article

# Factors Influencing the Occurrence of Onion Downy Mildew (*Peronospora destructor*) Epidemics: Trends from 31 Years of Observational Data

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**Abstract:** Onion downy mildew (ODM) caused by *Peronospora destructor* has been increasing annually in south-western Québec since the early 2000s, reaching 33% of affected onion fields in 2014. Using observational data collected over a period of 31 consecutive years, this study aimed to investigate the variations in ODM incidence and epidemic onset and identify the meteorological variables that influence its polyetic development. A logistic model was fitted to each ODM epidemic to estimate and compare the onset of epidemics on a regional basis. Results of this analysis showed that the first observation date, 10% epidemic onset ( $b_{10}$ ) and mid-time ( $b$ ) were, on average, 30.4, 15.1 and 11.3 days earlier in 2007–2017 than in 1987–1996. Results of a principal component analysis suggested that regional disease incidence was mostly influenced by the precipitation regime, the final regional disease incidence the previous year, and warmer temperature during the harvest period the previous fall. Subsequently, the data were divided in three periods of 10, 10 and 11 years, and a discriminant analysis was performed to classify each year in the correct period. Using a sufficient subset of five discriminating variables (temperature and rainfall at harvest the previous fall, winter coldness, solar radiation, and disease incidence the previous year), it was possible to classify 93.5% of the ODM epidemics in the period where they belong. These results suggest that *P. destructor* may overwinter under northern latitudes and help to highlight the need for more research on overwintering and for the development of molecular-based tools enabling the monitoring of initial and secondary inoculum.

**Keywords:** polyetic development; landscape epidemiology; climate change; long-term disease development

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## 1. Introduction

Over the last 20 years, the world production of onion (*Allium cepa* L.) more than doubled, moving from 2.4 million hectares of land in 1997 to 6.3 million hectares in 2017 [1]. In Canada, the provinces of Ontario and Québec grow more than 90% of the national production, with 2460 ha and 1938 ha,

respectively, dedicated to the production of dry bulb onions [2]. In Canada and elsewhere, onion crops are threatened by several diseases, including *Botrytis* leaf blight, *Stemphylium* leaf blight, purple blotch and downy mildew.

Onion downy mildew (ODM), caused by the obligate biotrophic oomycete *Peronospora destructor* (Berk.) Caspary, is a widespread disease that is often difficult to manage and can be destructive, with yield losses reaching up to 75% [3–6]. Weather conditions favoring *P. destructor* sporulation and infection were thoroughly studied in the 1980s, following severe disease outbreaks that occurred between 1977 and 1980 in Ontario (Canada) and in western and central New York [7,8]. The *P. destructor* sporulation process is dependent on daily cycles of light and darkness and is not initiated when infected onions are kept in continuous light or darkness [9]. Relative humidity greater than 95% and temperatures between 4 °C and 24 °C are required during the night cycle for sporulation [7]. When humidity is high from 20:00 onwards, sporulation may occur at temperatures as low as 10 °C, whereas the optimal temperature rises to 18 °C when humidity onset is after 3:00 [10]. After infection, a latency period of 13 days is observed at warmer temperature (25 °C/17 °C for day/night) and 15 to 17 days at cooler temperature (18 °C/10 °C for day/night) [11]. Mature sporangia are mostly dispersed by wind and there is no active release mechanism per se. However, *P. destructor* sporangia can be vigorously discharged into the air in response to a reduction of relative humidity [12,13].

This knowledge of sporulation and infection characteristics led, in the mid-1980s, to the development of DownCast, a forecaster for ODM [14,15]. The model provides a dichotomic output (0 or 1). Sporulation of *P. destructor* is predicted when (1) the mean temperature is below 24 °C between 08:00 and 20:00 the previous day; (2) the average night temperature is between 4 °C and 24 °C; (3) the relative humidity is greater than 95% between 02:00 and 06:00; and (4) no rain should occur after 02:00 [14]. This rule-based model is still in use in several growing regions, including Québec and Ontario, but despite its relative accuracy, the authors suggested that it could be improved. Hence, other models such as Onimil, Zwipero, DownCast-deVisser and Milioncast were developed to predict the risk of *P. destructor* sporulation or infection, or both [16–19].

Prediction systems are essential to make informed disease management decisions on a short-term basis. This type of decision-making is often referred to as tactical, because it takes place during the cropping seasons with the intention to protect the current crop [20]. In addition to tactical decisions, disease management must also be based on strategic decisions made at short, middle and very long terms [20]. Middle-term strategic decisions are defined at the field scale and include crop rotations, cultivar selection and seed treatments, whereas long-term strategic decisions are defined at larger scales in space (region, country, continent) and time (multi-year) [20]. Moreover, the long-term strategic decision is of most importance, because it allows growers to identify where integrated pest management (IPM) is needed for a particular disease and to anticipate when a given disease will pose a threat to a crop in a given production area [20]. To prevent or delay the development of plant diseases, it is thus recommended to characterize the disease progress on an annual basis and at multiple spatial and temporal scales [21,22]. Nevertheless, the epidemiology of plant diseases is generally studied over a few consecutive seasons because the available historical data collected over appropriate spatial and temporal scales are limited.

Amongst the epidemiological datasets covering a larger number of seasons, those for potato late blight caused by *Phytophthora infestans* are probably more numerous. In The Netherlands, for example, the analysis of a sequence of 47 potato late-blight epidemics has shown that the presence and level of late blight the previous year, the number of rainy days and relative humidity were important variables allowing for an accurate classification of disease intensity [23]. Similarly, historical data collected in Finland from 1933 to 2002 enabled changes in late blight incidence and epidemics onset to be linked to the increased frequency of rain and warmer temperature at the beginning of the growing season [24].

The importance of research on the relationship between climate change and plant diseases through studies conducted over an extended period of time is exacerbated by the speed at which changes are occurring. The latest forecasts regarding global warming suggest a global temperature increase between 1.5 °C and 2 °C over the next 50 years, especially in the northern and southern

regions [25]. However, the impact of climate change may vary with the geographic location of the production areas. The distribution and severity of late blight caused by *P. infestans* have increased with global warming and precipitation regime changes in the northern area [24], whereas the effect of climate change appears to be limited in tropical and subtropical regions [26].

In the Province of Québec (eastern Canada), the incidence of ODM has been increasing annually since the early 2000s, exceeding 30% of diseased onion fields in 2014. We hypothesize that changes in climatic conditions favor the overwintering of *P. destructor* and, therefore, the duration and precocity of ODM epidemics. Observational data collected over a period of 31 consecutive years are used to: (i) characterize the seasonal distribution patterns of ODM epidemics, (ii) determine if the onset of seasonal epidemics comes earlier and disease incidence is more important and (iii) identify the variables influencing the polyetic ODM development.

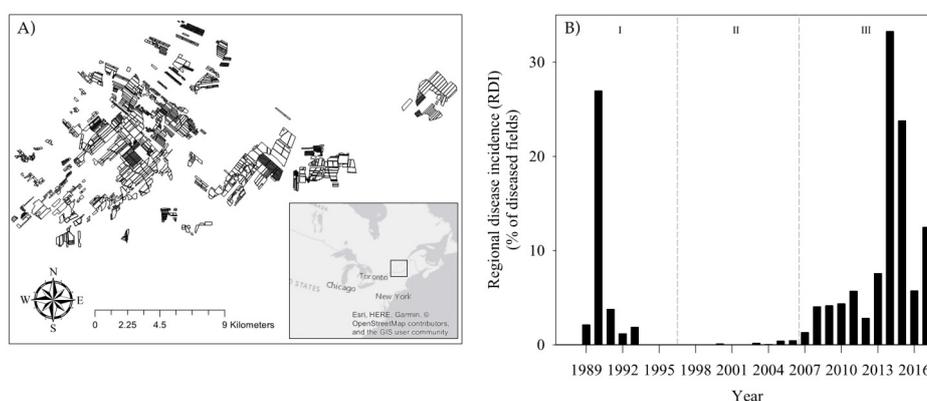
## 2. Material and Methods

### 2.1. Onion Production and Study Area

In Québec as in Canada, 80% of the areas dedicated to the production of alliums are dedicated to the production of dry bulb onions, while the remaining 20% are for garlic, leek and green onion. Most of the onion is grown from seed, whereas a small share of the production is grown from transplants or dry sets. Seeding or transplantation is generally performed in late April to early May, when the soil is thawed. Onions are sown about 2–2.5 cm below the soil surface, on 1.8 m wide beds, with double rows spaced 45 cm apart. Even though onions can be produced in various types of soil, the majority of the production is conducted in muck soils.

The study site (Municipalité Régionale de Comté des Jardins-de-Napierville) is located on the south shore of Montreal, surrounded by the Saint-Lawrence river to the north, the Adirondacks to the south and the Richelieu and Châteauguay rivers to the east and west, respectively. The cultivation area (~800 km<sup>2</sup>) is between latitude 45°03' N and 45°14' N and between longitude 73°42' W and 73°20' W. In this area, vegetable crops (mostly onion and lettuce) are grown in muck soil (chernozem), over slightly more than 10,000 ha (Figure 1A).

Climate in the study area is humid continental (Dfb, according to the Köppen classification), characterized by wet and warm summers (i.e., total precipitation from June to August is 293 mm on average, average temperature during the same months is 19.3 °C), cold and snowy winters (average temperature for December–March is −4.72 °C and average snow precipitation is 144.3 cm), with annual mean temperature of 6.6 °C, total precipitation of 799.6 mm and total snow precipitation of 169.3 cm. These climate statistics were compiled and published by the climate monitoring working group of the Ministère de l'Environnement et de la Lutte contre les changements climatiques du Québec (MELCC), for the Hemmingford Four Winds weather station (45°04'21" N, 73°39'29" W, 70 m).



**Figure 1.** Location of onion fields included in the study over the years (A) and regional disease incidence (RDI) of onion downy mildew (ODM) epidemics observed in the Napierville County for each of the 31 years of the dataset at the end of the growing season (B).

## 2.2. Field Sampling, Disease Incidence and Data Aggregation

The dataset analyzed in this study was constructed from the database of PRISME, a Québec bio-monitoring not-for-profit organization ([www.prisme.ca](http://www.prisme.ca)). The data were collected by agronomists, crop specialists and summer scouts from 1987 to 2017. Each year, scouting took place once a week from May to August in 122 fields on average per season, which represents ~70% of the total number of onion fields in the region. During scouting, observations on pests and diseases were made on at least 25 onion plants randomly selected in each field, including the presence/absence of ODM (1/0 binary data). The weekly data were then combined spatially to obtain a measure of regional disease incidence (RDI) expressed in percent, i.e., the percentage of infected fields. Thus, data are considered to be counts with an upper bound [27]. Furthermore, each field was given a value from a severity index (SEVI) ranging from 0 to 3: 0 = no ODM observation, 1 = less than 1%, 2 = between 1% and 5%, and 3 = greater than 5%. The first occurrence of ODM in the region each year was retrieved from the raw data and expressed in days since 1 May. To ensure that the dataset is representative of the region and there is no missing ODM outbreak, the RDI values were validated with experts from the Québec Ministère de l'Agriculture, des Pêcheries et de l'Alimentation and through the Phytosanitary Warning Network (Mario Leblanc, personal communication).

## 2.3. Weather-Related Variables

Data collected by the MELCC climate surveillance group at Hemingford Four Winds (45°04'21" N, 73°39'29" W, 70 m) were used in this study. Weather data from 1986 to 2017 were used to define four categories of variables, depending on whether they are: (1) related to sporulation (current growing season); (2) related to infection (current growing season); (3) favoring the production of overwintering inoculum (previous fall); or (4) related to overwintering (previous winter). The first two categories were mostly based on the conditions described by Hildebrand and Sutton [7,10,11,15,28]. Due to limited information available on the overwintering of *P. destructor*, the third and fourth categories of variables above were built on more general knowledge about peronosporales [23,24,29–32]. All variables used in this study are presented in Table 1.

Variables related to sporulation: These include the number of DownCast daily sporulation periods (DC, the number of days for which DownCast predicts a risk of sporulation) from May to August, and the number of hours with temperature between 4 °C and 24 °C at night (between 20:00 and 6:00) (HT4\_24N). Two variables which would prevent sporulation were also considered: the number of hours with temperatures greater than 28 °C at night (NHNT\_28) and the number of precipitation events (with at least 0.1 mm of rain) occurring between 20:00 and 6:00 (NSP).

Variables related to infection: The number of hours with relative humidity greater than 90% during the day (NHR\_90), the number of hours with temperature between 4 °C and 24 °C during the day (HT4\_24IP), the number of precipitation events (characterized by accumulation >0.25 mm) between 6:00 and 12:00 (DSP) and the number of precipitation events during the day (NREIP) are included in this category, as variables potentially enhancing infection. As two variables that would inhibit infection, the average solar radiation (RAD, in J m<sup>-2</sup>) and the number of hours with temperatures above 28 °C between 6:00 and 20:00 (NHDT\_28) are included in the same category.

Variables related to the production of overwintering inoculum: In this study, it was hypothesized that total rainfall during the harvest period (TRH) between 15 August and 15 October was amongst the most important variables influencing the formation of survival structures (oospores). The average and minimum temperatures during the harvest period (ATH and MTH) were also considered to be enhancing the production of oospores because higher temperature at harvest may lead to a longer period during which oospore production can occur.

Variables related to overwintering: Snow cover (SCOV, in cm), calculated from October 15 the previous year to 15 March the current year, was considered to contribute to the survival of oospores and volunteer plants in soil and cull piles, because snow acts as an insulating layer allowing a certain regulation of the soil temperature. Conversely, off season rainfall (OSRF), also calculated from 15 October to 15 March was considered to affect oospore survival because it may reduce the thickness of the snow cover or lead to the formation of ice. To measure winter severity, we use the Hellmann

number (HL), calculated as the sum of average daily temperatures below 0 °C from 15 October to 15 March [23]. The number of hours with temperatures below 0 °C, 5 °C and 10 °C were also used as indicators of coldness. Finally, we used the last RDI value the previous year (DS\_PY) and that the year before the previous year (DS\_P2Y), as variables of carryover from one or two years to the next.

**Table 1.** Description of the variables considered in this study.

Category	Variables	Definition
Dependent variables	RDI	Regional disease incidence (% of infected fields)
	DSI	Disease intensity (from 0 to 3)
Related to sporulation (Calculated from 1 May to 15 August)	DC	Number of DownCast sporulation periods
	NSP	Number of night precipitation events (between 24:00 and 6:00)
	HT4_24N	Number of hours with temperature between 4 °C and 24 °C (between 20:00 and 6:00)
	NHNT_28	Number of hours with temperatures above 28 °C (between 20:00 and 6:00)
Related to infection (Calculated from 1 May to 15 August)	RAD	Average solar radiation (J m <sup>-2</sup> )
	DSP	Number of morning precipitation events (between 7:00 and 12:00)
	NREIP	Number of precipitation events during infection period
	NHR_90	Number of hours with relative humidity above 90%
	HT4_24IP	Number of hours with temperature between 4 °C and 24 °C (between 6:00 and 20:00)
	NHDT_28	Number of hours with temperatures above 28 °C (between 6:00 and 20:00)
Related to production of overwintering inoculum (Calculated from 15 August to 1 October the previous year)	ATH	Mean temperature during harvest (°C)
	MTH	Minimum temperature at harvest (°C)
	TRH	Total rainfall at harvest (mm)
Related to overwintering (HL was calculated from November to March)	SCOV	Snow cover (mm)
	DS_PY	Final RDI previous year
	DS_P2Y	Final RDI the year before previous year
	HL	Hellmann number (sum of average daily temperatures below 0 °C) [23]
	OSRF	Off growing season rainfall (mm)

#### 2.4. Data Analysis

As changes in RDI are apparent over the 31 years (Figure 1B), the data were grouped into three periods of 10, 10 and 11 years (period I: 1987–1996, period II: 1997–2006 and period III: 2007–2017), representative of the bimodal distribution of RDI over time. For each of the variables studied, the data distribution was first tested for normality using the Shapiro–Wilk statistic. Since the data were not normally distributed, differences among mean values of the three periods for RDI and weather-related variables (Table 1) were assessed with the Kruskal–Wallis non-parametric test, followed by a Dwass, Steel and Critchlo–Fligner two-sided multiple pairwise comparison test (significance level  $\alpha = 0.05$ ).

Then, for each of the 31 years with enough ODM incidence, the seasonal ODM epidemic was studied by fitting a logistic model to the disease progress curve built on the cumulative RDI, expressed as a proportion of the maximum:

$$Y = \frac{K}{1 + e^{-r*(t - b)}} \quad (1)$$

where the quantity  $Y$  is the cumulative RDI,  $t$  is the time (in days, for a given season),  $K$  is the theoretical upper limit (asymptote) for  $Y$ ,  $r$  is the rate of growth and  $b$  is a time offset at which  $Y$  is equal to half of the maximum value (mid-time). The 10% epidemic onset ( $b_{10}$ ), at which  $Y$  is equal to 10% of the maximum value, was derived from the fitted model. The goodness-of-fit of the model was

assessed by the root mean square error (RMSE) and the coefficient of determination ( $R^2$ ). A Wilcoxon exact non-parametric test (significance level  $\alpha = 0.05$ ) was performed to determine whether the 10% epidemic onset, mid-time and other model parameter estimates were significantly different between the first and third periods, where the RDI modes are found.

Spearman's rank-based correlation coefficients were computed between weather-related variables and the response variables (RDI, DSI) over the 31 years. The resulting correlation matrix was used in a principal component analysis (PCA), to investigate the relationships between RDI or DSI and the weather-related variables and among the weather-related variables themselves.

Using periods I, II and III as classes, discriminant analyses were performed to identify the variables (excluding RDI and DSI) that influenced the ODM polyetic development differently across the three periods. A discriminant analysis was performed with all the weather-related variables and another with a reduced number of them (i.e., a sufficient subset of discriminating variables), retained at the end of a stepwise procedure. The rank-transformed data were used in these analyses. The outputs include the probabilities of classification of the years in the three periods (I, II or III), in an attempt to predict higher or lower ODM occurrence from the weather-related variables.

In the application of multivariate statistical methods (e.g., PCA, discriminant analysis) with time-series data, joining the years in chronological order in biplots facilitates the interpretation of results and such a temporal walk may allow the detection of atypical years within a period in the case of the PCA [33]. The statistical analyses described above were carried out with procedures NLIN, UNIVARIATE, NPAR1WAY, CORR, PRINCOMP, DISCRIM and STEPDISC from SAS/STAT V9.4 (SAS Institute Inc., Cary, NC, USA).

### 3. Results

Regional disease incidence values in the years 1987–2017 varied from 0 to 33.25% and form a bimodal distribution with one peak in 1990 and the other in 2014 (Figure 1B). The ODM was present in five years out of 10 in period I (mean RDI: 3.59%,  $SE = 2.63$ ), five years out of 10 in period II (mean RDI: 0.11,  $SE = 0.05$ ), and 11 years out of 11 in period III (mean RDI: 9.55,  $SE = 3.17$ ). For the majority of the variables, the null hypothesis of a normal distribution, was rejected according to the Shapiro–Wilk test. The Kruskal–Wallis test shows a significant difference in the mean RDI value among the three periods ( $p = 0.0002$ ). The multiple pairwise comparison test then found a significant difference between periods I and III ( $p = 0.0102$ ) as well as between periods II and III ( $p = 0.0003$ ), but not between periods I and II ( $p = 0.5708$ ) (Table 2).

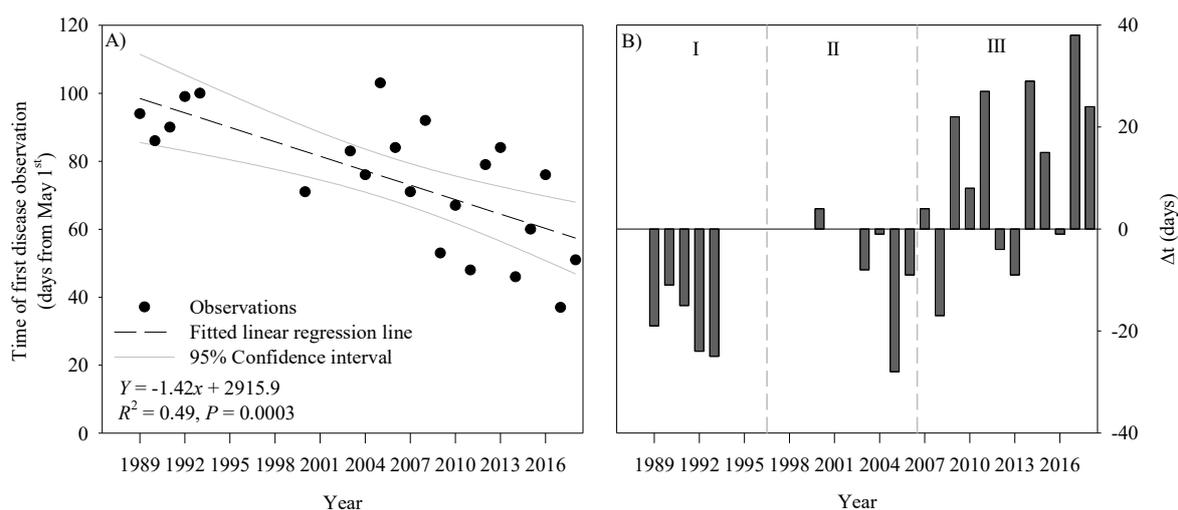
There are also significant differences among the three periods in the mean value of the weather-related variables, especially the ones related to production and survival of overwintering inoculum. For these, the Kruskal–Wallis test shows significant differences among periods for the average and minimum temperature during harvest and the total rainfall during harvest ( $p = 0.0302$ ,  $0.0015$  and  $0.0008$ , respectively) (Table 2). In summary, the average and minimum temperatures were significantly warmer while precipitation was more abundant in period III than in period I (Table 2). For the variables related to overwintering, the Kruskal–Wallis test shows significant differences among periods for the disease statuses the previous year and the previous two years ( $p = 0.0002$  and  $0.0002$ , respectively), while the Hellmann numbers (HL) suggest warmer winters for period III compared to period I ( $p = 0.0084$ ) (Table 2). For the variables related to sporulation, differences among periods are significant for the number of DownCast periods ( $p = 0.0072$ ), while significant differences are also found for solar radiation in the category of variables related to infection ( $p < 0.0001$ ) (Table 2).

The first ODM outbreak was reported, on average, 75 days after 1 May (Figure 2A). The correlation between year of the survey and time of the first outbreak is negative and significant ( $r = -0.700$ ;  $p = 0.0003$ ) (Figure 2A). More specifically, the first disease outbreak was reported, on average, 93.8, 84.3 and 63.4 days after 1 May, during the first, second and third periods, respectively (Figure 2B). The fitting of logistic models confirms this trend in ODM seasonal epidemics (Figure 3A, Table 3). In addition to earlier disease outbreaks, the 10% epidemic onset ( $b_{10}$ ) and mid-time ( $b$ ) were 15.1 and 11.3 days earlier in period III than in period I ( $p = 0.0102$  and  $p = 0.0255$ ) (Figure 3B, C).

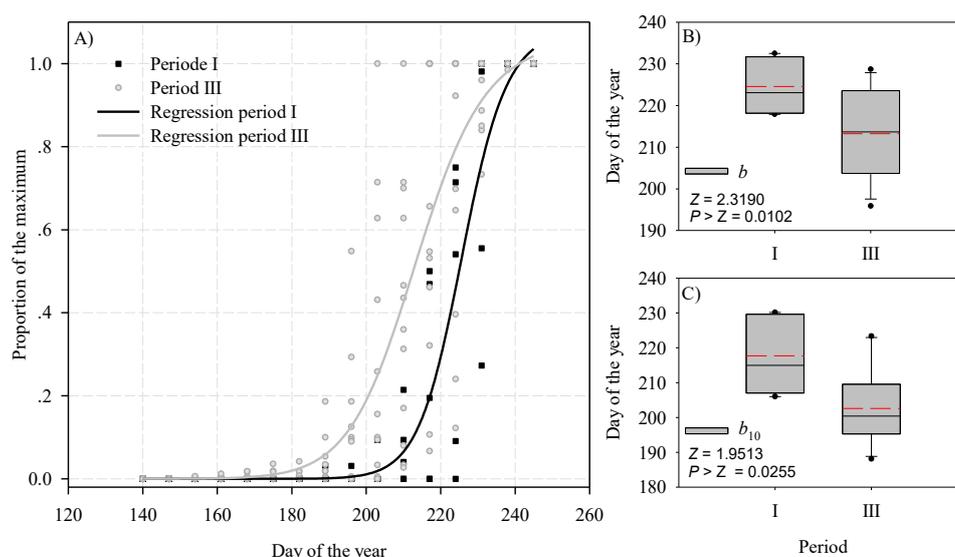
**Table 2.** Mean values of regional disease incidence (RDI) and weather-related variables, and results of the Kruskal–Wallis test (observed value of the test statistic and corresponding probability of significance).

Variables *	Period **			$\chi^2$	<i>p</i>
	I	II	III		
RDI	3.6 <sup>a</sup>	0.1 <sup>a</sup>	9.6 <sup>b</sup>	17.20	0.0002
DC	33.7 <sup>b</sup>	22.0 <sup>a</sup>	20.18 <sup>a</sup>	9.87	0.0072
NSP	52.6	66.9	80.5	4.73	0.0941
HT4_24N	1245.3	1207.5	1227.7	0.75	0.6867
NHNT_28	0.4	0.3	0.6	0.01	0.9945
RAD	15.94 <sup>b</sup>	15.77 <sup>b</sup>	12.32 <sup>a</sup>	20.45	<0.0001
DSP	79.3	82.6	107.5	5.33	0.0699
NREIP	33.4	34.1	47.6	4.11	0.1284
NHR_90	413.0	486.6	468.6	5.23	0.0732
HT4_24IP	451.5	447.2	446.5	0.94	0.624
NHDT_28	45.2	41.9	41.5	0.11	0.9463
ATH	17.30 <sup>a</sup>	18.42 <sup>a,b</sup>	18.81 <sup>b</sup>	6.99	0.0302
MTH	7.28 <sup>a</sup>	9.5 <sup>b</sup>	10.5 <sup>b</sup>	13.05	0.0015
TRH	42.6 <sup>a</sup>	90.9 <sup>b</sup>	104.82 <sup>b</sup>	14.15	0.0008
SCOV	154.6	146.4	158.7	0.06	0.9683
DS_PY	3.6 <sup>a</sup>	0.1 <sup>a</sup>	8.5 <sup>b</sup>	16.92	0.0002
DS_P2Y	3.6 <sup>a</sup>	0.1 <sup>a</sup>	7.99 <sup>b</sup>	16.76	0.0002
HL	-111.7 <sup>b</sup>	-98.97 <sup>a,b</sup>	-94.46 <sup>a</sup>	9.56	0.0084
OSRF	330.1	289.7	298.4	0.12	0.9424

\* Mean values with different letters within the same row are significantly different according to the Dwass, Steel and Critchlo–Fligner two-sided multiple pairwise comparison test (significance level  $\alpha = 0.05$ ). \*\* Period I include the years from 1987 to 1996, period II from 1997 to 2006, and period III from 2007 to 2017.



**Figure 2.** Plots against Year for (A) the earliest time of ODM observation from 1 May, with linear regression analysis results, and (B) the difference between the average first observation date and the first observation date for each year during which ODM was observed.



**Figure 3.** (A) Disease progress curves for the first and third ODM periods. Box plots of (B) model parameter estimate  $b$ , which represents the time (in days) at which seasonal ODM incidence is half of its maximum value (mid-time) and (C)  $b_{10}$ , the time (in days) when seasonal ODM incidence is equal to 10% of the maximum value (10% epidemic onset). Period I include the years 1987–1996, and period III, 2007–2017. In each box plot, the horizontal black lines, from bottom to top, represent the 10th, 25th, 50th (median), 75th and 90th percentiles, the red dashed line represents the mean and a black circle represents an outlier. The Z statistic and associated  $p$ -value are for the Wilcoxon exact test (significance level  $\alpha = 0.05$ ).

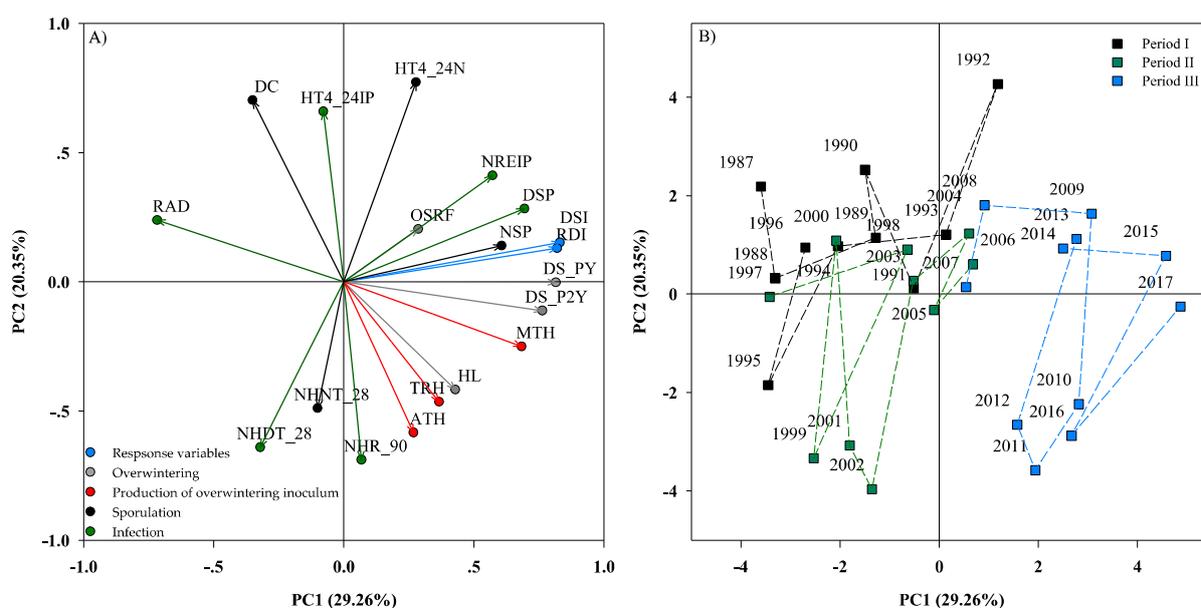
Through correlations, the PCA was used to evaluate the relationships between weather-related variables and RDI or DSI over the 31 years. The eigenvalues calculated for the correlation matrix correspond to the proportions of dispersion (after standardization) explained by the principal components (PCs), the coefficients of the corresponding eigenvectors indicating the relative importance of each predictor in the composition of the PCs. Taken together, the first three PCs explain 60.3% (PC1: 28.9%, PC2: 20.3% and PC3: 11.1%) of the total dispersion (Table 4). The eigenvectors of the first principal component had values ranging from  $-0.310$  to  $0.355$ , with the highest and lowest value corresponding to disease incidence the previous year (DS\_PY) and solar radiation (RAD), respectively. The eigenvectors of the second principal components had values ranging from  $-0.352$  to  $0.394$ , with the highest and lowest value corresponding to the number of hours with temperature between  $4\text{ }^{\circ}\text{C}$  and  $24\text{ }^{\circ}\text{C}$  during the day (HT4\_24IP) and the number of hours with relative humidity greater than 90% (NHR\_90), respectively (Table 4). While PC1 was largely associated with variables related to overwintering, PC2 was more related to temperature and relative humidity associated with infection and sporulation (Table 4).

**Table 3.** Summary of the logistic model (Equation (1)) fitting results for each of the 31 years (1987–2017) with enough ODM incidence.

Year	Parameter <sup>a</sup>	Estimate	SE	Approximate 95% Confidence Limits		Model <i>p</i> -Value	Year	Parameter	Estimate	SE	Approximate 95% Confidence Limits		Model <i>p</i> -Value
<b>1989</b>	<i>k</i>	1.024	0.024	0.972	1.077	0.0001	<b>2010</b>	<i>k</i>	1.019	0.036	0.941	1.098	0.0001
	<i>r</i>	0.187	0.017	0.150	0.225			<i>r</i>	0.151	0.024	0.099	0.204	
	<i>b</i>	217.900	0.594	216.600	219.200			<i>b</i>	202.800	1.260	200.100	205.500	
<b>1990</b>	<i>k</i>	1.028	0.017	0.990	1.065	0.0001	<b>2011</b>	<i>k</i>	1.040	0.049	0.935	1.145	0.0001
	<i>r</i>	0.274	0.021	0.228	0.321			<i>r</i>	0.141	0.026	0.084	0.198	
	<i>b</i>	223.100	0.326	222.400	223.800			<i>b</i>	206.400	1.594	202.900	209.800	
<b>1991</b>	<i>k</i>	1.020	0.022	0.973	1.068	0.0001	<b>2012</b>	<i>k</i>	1.000	0.001	1.000	1.000	0.0001
	<i>r</i>	0.214	0.020	0.171	0.257			<i>r</i>	2.021	0.013	1.994	2.048	
	<i>b</i>	218.400	0.513	217.300	219.500			<i>b</i>	195.900	1.32×10 <sup>-9</sup>	195.900	195.900	
<b>1992</b>	<i>k</i>	1.012	0.025	0.959	1.066	0.0001	<b>2013</b>	<i>k</i>	1.011	0.017	0.975	1.047	0.0001
	<i>r</i>	0.663	0.196	0.240	1.086			<i>r</i>	0.412	0.032	0.344	0.480	
	<i>b</i>	232.500	0.496	231.400	233.600			<i>b</i>	228.700	0.255	228.100	229.200	
<b>1993</b>	<i>k</i>	1.000	0.001	1.000	1.000	0.0001	<b>2014</b>	<i>k</i>	1.072	0.053	0.957	1.187	0.0001
	<i>r</i>	1.993	0.008	1.976	2.009			<i>r</i>	0.164	0.022	0.116	0.211	
	<i>b</i>	230.900	0.001	230.900	230.900			<i>b</i>	224.800	1.089	222.500	227.200	
<b>2006</b>	<i>k</i>	0.954	0.030	0.891	1.018	0.0001	<b>2015</b>	<i>k</i>	1.057	0.040	0.970	1.144	0.0001
	<i>r</i>	0.630	0.340	-0.104	1.364			<i>r</i>	0.128	0.015	0.095	0.160	
	<i>b</i>	201.400	0.999	199.200	203.500			<i>b</i>	213.400	1.176	210.900	216.000	
<b>2007</b>	<i>k</i>	1.005	0.018	0.966	1.043	0.0001	<b>2016</b>	<i>k</i>	1.006	0.021	0.961	1.051	0.0001
	<i>r</i>	0.420	0.060	0.289	0.550			<i>r</i>	0.560	0.093	0.359	0.760	
	<i>b</i>	208.000	0.423	207.100	208.900			<i>b</i>	226.000	0.406	225.100	226.900	
<b>2008</b>	<i>k</i>	1.014	0.016	0.979	1.050	0.0001	<b>2017</b>	<i>k</i>	1.121	0.041	1.032	1.210	0.0001
	<i>r</i>	0.262	0.023	0.213	0.312			<i>r</i>	0.098	0.007	0.083	0.112	
	<i>b</i>	213.900	0.400	213.100	214.800			<i>b</i>	219.900	1.131	217.400	222.300	
<b>2009</b>	<i>k</i>	1.025	0.032	0.956	1.094	0.0001							
	<i>r</i>	0.150	0.015	0.118	0.182								
	<i>b</i>	217.900	0.831	216.100	219.700								

<sup>a</sup>Parameters of the logistic model used in this study.

Graphically and accordingly, the RDI and DSI vectors in the PC2-PC1 biplot go in the same direction as those for disease status the previous year (DS\_PY) and the previous two years (DS\_P2Y), minimum temperature at harvest (MTH) and number of morning precipitation events (DSP), whereas the solar radiation (RAD) vector points in the opposite direction (Figure 4A). In the year space (Figure 4B), it is possible to follow the chronology of events along PC1, with the period I years on the left, the period III years on the right and the period II years in-between; PC2 tends to show fluctuations among years within a period.



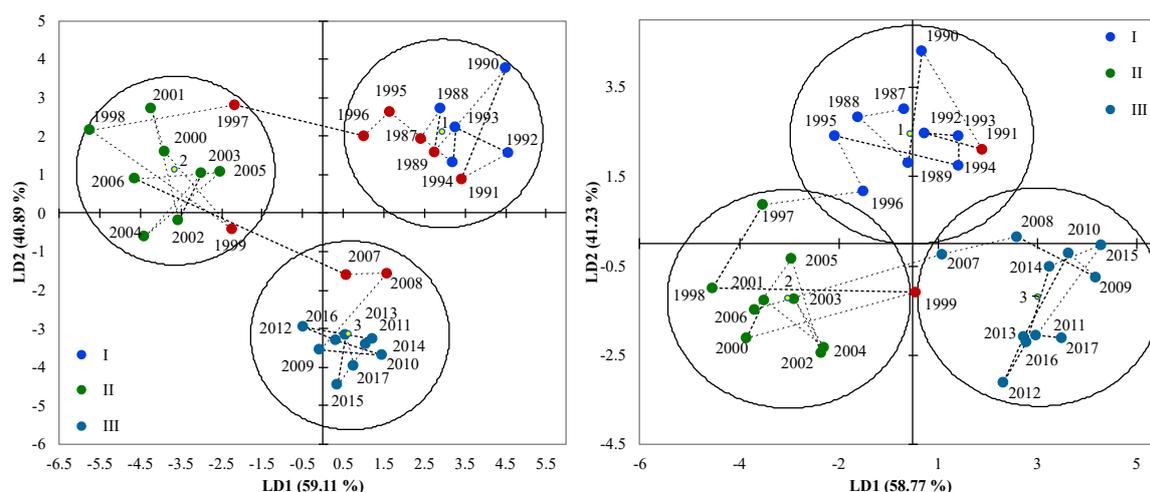
**Figure 4.** Principal component analysis (PCA) biplots obtained by using the first two principal components (A) in the variable space and (B) in the year space, where consecutive years are linked to allow following the temporal walk.

When using all the weather-related variables in the discriminant analysis, only 50% of the years belonging to period I, 80% of the years belonging to period II and 81.8% of the years belonging to period III are correctly classified (Figure 5A). Overall, the achieved classification accuracy is 70.6%. At the end of the stepwise procedure, five variables (MTH, DS\_PY, HL, TRH and RAD) were retained as a sufficient discriminating subset (Table 5). Using these five variables, 90%, 90% and 100% of the years belonging to the first, second and third ODM periods are correctly classified (Figure 5B), and the achieved overall classification accuracy is 93.5%.

**Table 4.** Composition of the eigenvectors (as linear combinations of variables) for the first three principal components in the PCA.

Categories	Variables	Principal Components		
		1	2	3
Related to sporulation	DC	-0.1501	0.3595	-0.1119
	NHNT_28	-0.0422	-0.2494	0.2626
	HT4_24N	0.1225	0.3935	-0.0859
	NSP	0.258	0.0695	0.3646
	DSP	0.2905	0.1403	0.4098
Related to infection	RAD	-0.3104	0.1242	0.187
	NHDT_28	-0.1389	-0.3254	0.0754
	HT4_24IP	-0.0299	0.3353	-0.2817
	NHR_90	0.0295	-0.3518	0.0737
	NREIP	0.2409	0.2085	0.4248

Related to production of overwintering inoculum	ATH	0.1088	-0.2944	-0.1261
	TRH	0.1538	-0.2353	-0.1137
	MTH	0.2930	-0.1287	-0.1455
Related to overwintering	OSRF	0.1171	0.1021	0.3673
	HL	0.1821	-0.2124	0.0499
	DS_P2Y	0.3175	-0.059	-0.1326
	DS_PY	0.3418	0.0015	-0.1674
Cumulative variation accounted for (%)	RDI	0.3499	0.0668	-0.1576
	DSI	0.3549	0.0776	-0.2156
		28.93	49.23	60.25



**Figure 5.** Discriminant analysis results presented graphically in biplots of the second linear discriminant variable (LD2) against the first (LD1). The blue, green and turquoise points represent the years correctly classified in periods I, II and III, respectively. The red points indicate the years that are misclassified. A) All the weather-related variables are used, and the overall correct classification rate is 70.6%. B) The discriminating subset of five variables (MTH, DS\_PY, HL, TRH, RAD) found to be sufficient at the end of the stepwise procedure is used: 93.5% of the years are correctly classified within the three ODM periods.

**Table 5.** Weather-related variables retained in the stepwise discriminant analysis procedure, applied to identify the smallest sufficient set of discriminating variables for periods I, II and III, and the corresponding statistics.

Variables <sup>a</sup>	F-Value <sup>b</sup>	p > F	Partial R <sup>2</sup> <sup>b</sup>	Wilks' Lambda <sup>c</sup>	p < Lambda
RAD	29.570	<0.0001	0.6787	0.3213	<0.0001
DS_PY	10.310	0.0005	0.4331	0.1821	<0.0001
MTH	15.750	<0.0001	0.5479	0.0823	<0.0001
TRH	8.370	0.0016	0.4011	0.0493	<0.0001
HL	2.380	0.1145	0.1652	0.0412	<0.0001

<sup>a</sup> See Table 1 for the description of the variables. <sup>b</sup> An F-test is performed to assess whether the inclusion of a variable in the discriminating subset reinforces the discrimination significantly or not; a 0.15 significance level to enter was used. The outcome of the F-test (enter, yes/no) is related to the partial R<sup>2</sup>, which is indicative of the increase in size (%) of the difference among vectors of mean values after inclusion of the variable considered. <sup>c</sup> Wilks' Lambda is a likelihood-ratio test statistic used to compare vectors of mean values; it is used in various contexts, including multivariate analysis of variance (MANOVA) and discriminant analysis.

#### 4. Discussion

Although the local conditions for *P. destructor* infection and sporulation were thoroughly studied in the 1980s [7,10–12,14,15,28,34], the processes underlying ODM seasonal establishment are poorly understood. Results of the analyses of scouting data collected from 1987 to 2017 in our study allowed a quantitative description of the ODM epidemics in the long term over time and at a regional scale. The epidemics occurring during period III (2007–2017) were more severe than those during period I (1987–1996) and were characterized by the first ODM observation dates that were earlier in the year (30.4 days on average). The first disease observation date is a valuable indicator of change in disease epidemiology but may not be representative of the seasonal establishment of the disease in a given area. For this reason, we fitted models to regional disease progress curves to calculate and compare 10% epidemic onset and mid-time for the three ODM periods. Results of the non-linear regression analysis (logistic model fitting) are consistent with those for the first observation dates, as the 10% epidemic onset and mid-time are, respectively, 15.1 and 11.3 days earlier in 2007–2017. The incidence of ODM during the transition between the second and third periods was too low for seasonal disease establishment, so that no logistic model was fitted for the corresponding years. However, these observations are of interest, as they heralded a shift in the polyetic ODM development. A similar trend was observed for potato late blight caused by *P. infestans* in Finland. Using a historical dataset from 1933 to 2002, Hannukkala et al. [24] showed that late blight epidemics started two to four weeks earlier in the years 1996–2002 than in 1933–1962. This trend was later confirmed for the 2002–2012 period [30], and a similar trend was also reported in Sweden for 1983–1992 compared to 1993–2012 [35].

As for other *Peronosporaceae*, *P. destructor* has long been thought to be a periodically introduced oomycete because of multiyear ODM epidemics followed by multiyear absence of the epidemic [36]. For these pathogens, atmospheric transport of sporangia is considered to play a major role in their long-distance spread. Thus, the presence of periodically introduced oomycetes in northern latitudes largely depends on sporangia dispersal from outbreaks occurring in the South [37–39]. Their sporadic presence in northern areas may be the result of a lack of local production of oospores or simply because they cannot survive the rigor of winters beyond a certain latitude. This is the case of *Pseudoperonospora cubensis*, which is not known to overwinter in the field above 30° latitude North [39–41]. Long-distance dispersal is subjected to several factors (e.g., presence of susceptible hosts, anthropogenic trades), but it is reasonable to expect that the closer the overwintering source, the earlier and the more frequent and severe the epidemics will be. Our results are supportive of the hypothesis of a continuous shift poleward of plant pathogens, possibly because of global climate change [42]. While *P. destructor* mainly spreads by aerial dispersal, climatic conditions are likely to determine the subsequent establishment of the disease in a given area. Hence, our results point to an adaptation of the pathogen with respect to the production and survival of overwintering inoculum under the south-western latitudes of Québec.

An increasing number of studies provide ever more accurate predictions of the effects of climate change on plant diseases [26,43–48], but studies remain limited and constrained by the availability of data [49,50]. Moreover, when available, the observations may come from several sources and in different types (discrete, categorical or continuous). Thus, it is often impossible to choose the appropriate scale (field, farm, county, country or continent). In our study, even though the original observations were made at the plant level, there is one line of data per field per date in the database. It follows that the fields are considered as the units of infection and the epidemics are studied at two nested time scales (i.e., the year and the day within a year), enabling a smooth shift to multi-year regional disease level [51]. In their long-term analysis of potato late blight epidemics, Zwankhuizen and Zadoks [23] had to merge qualitative and quantitative observations from several sources (annual reports of plant protection service, journal articles and unpublished data) and accept some arbitrariness of classification, to finally work at an aggregation level of years and countries in time and space [23]. To investigate the poleward shift of pests and plant pathogens in response to global warming, Bebbler et al. [42] used data from the CABI (Commonwealth Agricultural Bureau) distribution maps which were also aggregated at the country level.

The study of the polyetic development of plant diseases and their interactions with climate change is highly relevant in a context of changing agricultural landscape. As a result, diseases may emerge where they were non-existent and the frequency of occurrence of existing diseases may increase, but also the status of plant pathogens known to be periodically introduced may change and become endemic. Among the factors that can influence the distribution of plant pathogens or the magnitude of seasonal epidemics, temperature and precipitation regimes are of most importance. For some diseases, it is realistic to expect that increasing temperature favors overwintering and increases the number of seasonal disease cycles, while changes in precipitation regime might enhance (or disfavor) infection processes [50]. Our PCA results suggest that regional disease incidence (RDI) was mostly influenced in a season by precipitation (NSP, DSP), but not by diurnal or nocturnal temperature (NHNT\_28, HT4\_24N, NHDT\_28, HT4\_24IP). Because *P. destructor* is known to be more aggressive at lower temperatures (i.e., favorable temperatures are between 4 °C and 24 °C) [7], whereas sporangia germination is much lower above 26 °C and completely inhibited above 28 °C [14], it was expected that these temperature variables would have been important. The PCA results also suggest that regional disease incidence was influenced by the variables related to the production of oospores and their survival. The disease statuses the previous year and the previous two years (DS\_PY, DS\_P2Y) appear to be an important source of carryover, mainly because the larger the number of ODM cases, the higher the probability of oospore production. Warmer temperature at harvest time the previous year (MTH) was also shown to be an important factor. Higher temperatures towards the end of the growing season is thought to give the pathogen additional time to form oospores, possibly in larger quantity.

The meteorological variables that vary the most among the three periods are related to oospore production and survival. The mean and minimum temperatures during harvest (ATH and MTH) were higher, precipitation during harvest (TRH) was more abundant, and the winter was less severe in period III than in period I. Using the subset of five variables retained at the end of the stepwise procedure (i.e., MTH and TRH: temperature and precipitation at harvest the previous fall; HL: severity in winter; RAD: solar radiation and DS\_PY: disease incidence the previous year), the discriminant analysis results improved considerably from 70.6% to 93.5% correct classification. Except for solar radiation, which is known to affect negatively the viability of oomycete sporangia [10,12,52], the variables influencing RDI the most are variables related to the production and survival of overwintering structures.

The role of oospores in the epidemiology of ODM is under-documented. It is known that *P. destructor* produces oospores in natural conditions and these oospores can be long-lasting in the soil [53,54]. In an experiment conducted over 25 consecutive years, McKay [53] found that oospores were able to germinate up to 25 years after their production. In the same study, it was shown that oospores needed an incredibly long maturation period, as the first observation of germination occurred after four years and reached the maximum germination rate after seven years [53]. Although it would be surprising that this oomycete produced oospores adapted for such a long-term survival for no apparent reason, their potential as a source of primary inoculum remains ambiguous. There is no clear evidence that oospores present in soil can lead to infection [53,55,56]. Alternatively, systemically infected tissues (mainly infected immature bulbs) can be an important source of primary inoculum [34,56,57]. Whether it is from oospores or infected crop residues, the results obtained in this study suggest that variables favoring the production and survival of overwintering structures may play an important role in seasonal ODM epidemics.

The assumption of overwintering of *P. destructor* inoculum entails changes in tactical and strategic decision-making. The information on overwintering inoculum could become an important component of tactical decisions, for example, to plan the deployment of spore-trapping networks. In addition, the disease status the previous year and the harvest and winter weather conditions can also be used as baseline information for risk prediction models during the current year. The implication of this assumption is also meaningful for short-term strategic decisions because the presence of inoculum in soils is likely to influence the planning of crop rotations and the selection of cultivars and cropping systems [20].

In general, the use of observational data implies the acceptance of greater uncertainty in the data, the potential introduction of bias due to multiple data sources, and the acceptance of correlations instead of understanding causation [42,50]. However, observational data and their analysis can reveal significant trends and influence long-term tactical decisions. Our main results are that ODM epidemics in south-western Québec tend to come earlier and more frequently, and that the increased disease incidence is linked to weather variables related to overwintering and disease carryover from one growing season to the next. Either there is production and survival of overwintering inoculum under the latitudes of south-western Quebec, or the production areas where survival is possible are closer than before. Finally, this study also contributes to long-term tactical decisions by highlighting the need for more research on overwintering and for the development of molecular-based tools enabling the monitoring of initial and secondary inoculum.

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