Association Between Weather Variables, Airborne Inoculum Concentration, and Raspberry Fruit Rot Caused by *Botrytis cinerea*

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ABSTRACT

Botrytis fruit rot (BFR), one of the most important diseases of raspberry (*Rubus* spp.), is controlled primarily with fungicides. Despite the use of fungicides, crop losses due to BFR are high in most years. The aim of this study was to investigate the association between airborne inoculum, weather variables, and BFR in order to improve the management of the disease as well as harvest and storage decisions. Crop losses, measured as the percentage of diseased berries during the harvest period, were monitored in unsprayed field plots at four sites in three successive years, together with meteorological data and the number of conidia in the air. Based on windowpane analysis, there was no evidence of

correlation between crop losses and temperature, vapor pressure deficit, wind, solar radiation, or probability of infection. There were significant correlations between crop losses and airborne inoculum and between crop losses and humidity-related variables, and the best window length was identified as 7 days. Using 7-day average airborne inoculum concentration combined with 7-day average relative humidity for periods ending 6 to 8 days before bloom, it was possible to accurately predict crop losses (R^2 of 0.86 to 0.89). These models could be used to assist with managing BFR, timing harvests, and optimizing storage duration in raspberry crops.

Botrytis cinerea (teleomorph *Botryotinia fuckeliana* (de Bary) Whetzel) is a facultative fungal saprophyte with a wide range of host plants from different genera and families, including several crop, weed, and wild plant species (Carisse 2016). In addition, *Botrytis cinerea* is present worldwide wherever suitable hosts are grown (Dean et al. 2012) and causes damage to nursery plants, field- and greenhouse-produced fruit and vegetable crops, field crops, and stored and in-transit products (Carisse 2016).

Raspberry varieties are members of the Rosaceae (rose) family. In eastern Canada, raspberry (*Rubus idaeus*) is a relatively minor but valuable crop, mostly because it contains ellagic acid, a potent anticarcinogenic and antimutagenic compound (Duthie 2007). Most of the raspberry fruit grown in eastern Canada are sold for the fresh market and, hence, the quality of the harvested berries is very important. Gray mold, *Botrytis* fruit rot (BFR), and *Botrytis* cane blight, all caused by *B. cinerea*, are endemic diseases present in most raspberry plantings in Canada (Agriculture and Agri-Food Canada 2016). *B. cinerea* infects blossoms and fruit and results in rotted and dried berries, reducing both berry quality and marketable crop yield. In general, *Botrytis* cane blight causes fewer economic losses than fruit rot does (Xu et al. 2009).

Most of what is known about the ecology of *B. cinerea* and the epidemiology of *Botrytis*-induced berry diseases is derived from studies on strawberry and grape (Carisse 2016; Williamson et al. 2007). In raspberry, similar to other berry crops, *B. cinerea* infects petals, flower stalks, fruit caps, and fruit. Infected berries become soft and light brown and, if they remain on the plant, they generally dry up and become covered with a gray, dusty powder made of *B. cinerea* conidia. These spores contribute to the secondary infection of fruit, primocanes, and other green tissues. During wet and warm seasons, specifically in years with prolonged rainy and cloudy

periods during bloom or harvest, *B. cinerea* can cause considerable crop losses (Jarvis 1962b).

B. cinerea overwinters as small sclerotia on primocanes and as mycelia on dead leaves and mummified fruit. In the spring, sclerotia and mycelia produce conidia, which are spread by wind. The optimum conditions for production of conidia are temperatures between 15 and 22°C and high relative humidity (RH) (Jarvis 1962a) or tissue wetness (Sosa-Alvarez et al. 1995). However, conidia can also be produced at temperatures as low as 5°C, depending on the duration of the period of high RH or tissue wetness (Sosa-Alvarez et al. 1995). Because conditions conducive to conidia production are often present, airborne *B. cinerea* conidia are ubiquitous. However, their concentration in the air fluctuates depending on the prevailing weather conditions and the phenological stage of the crop (Blanco et al. 2006; Carisse et al. 2014; Jarvis 1962a). Once deposited on susceptible tissues, conidia germinate and penetrate host tissues within only a few hours when a film of water is present. The best conditions for infection are temperatures between 20 and 27°C and free moisture on the host tissues from rain, dew, fog, or irrigation water. Infection can occur at lower temperatures provided that the host tissues remain wet for long periods. Raspberry fruit are susceptible during bloom and during fruit ripening. Even though most fruit infections occur during bloom, symptoms become visible only near harvest. During bloom, *B. cinerea* colonizes flower parts, becomes established in the receptacle of the young fruit, and remains quiescent until the fruit begins to mature. Consequently, the most critical period for applying fungicides is during bloom. Despite the common practice of spraying a fungicide at 10, 50, and 80% bloom, losses can be as high as 100% (Ellis et al. 2008). The necrotrophic growth habit of *B. cinerea* (it kills living cells and colonizes the dead tissue) means that, depending on the availability of dead or senescent plant materials and on weather conditions, inoculum of *B. cinerea* can progress more or less rapidly, influencing the amount of inoculum present when raspberry plants are becoming susceptible (flowering period). This means that the critical periods for raspberry gray mold may occur before flowering. These factors, along with the difficulty of monitoring the disease

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before losses occur and the expanding market for fresh fruit, have accentuated the need for disease risk indicators to help manage BFR.

Various types of risk indicators were developed for *Botrytis* gray mold on strawberry and grape. Most risk indicators are weather based and were developed from controlled-conditions experiments and not translated into practical disease management tools (Broome et al. 1995; Bulger et al. 1987; Nair and Allen 1993). Nevertheless, these risk indicators are useful tools for estimating how favorable the environment is, mainly in terms of temperature and wetness, for flower infections by *B. cinerea*. An expert system was developed for *Botrytis* bunch rot of grape (Ellison et al. 1998a) to help with the timing of fungicide sprays but, following field validation, the system only slightly improved application timing in comparison with standard grower practices (Ellison et al. 1998b). Recently, a mechanistic model was developed to predict the risk of grapevine infection by *B. cinerea* (González-Domínguez et al. 2015). The model was designed to predict the severity of epidemics (mild, intermediate, or severe), and, when validated under field conditions, the model was reliable and correctly classified 17 of 21 epidemics. Xu et al. (2012) evaluated a strawberry gray mold (*B. cinerea*) weather-based prediction model for its ability to predict raspberry fruit rot. They reported that the incidence of flower infection and fruit rot was considerably higher on raspberry than on strawberry. However, their model developed for strawberry significantly over-estimated infection of raspberry flowers. Furthermore, they reported that, for their four datasets, the general trend of predicted raspberry infection did not follow the observed pattern. They concluded that variables other than temperature and humidity may need to be considered for predicting risk of raspberry infection caused by *B. cinerea* (Xu et al. 2012).

The overall objective of this study was to investigate the empirical associations (relationships) between weather or *B. cinerea* airborne conidia concentration during the period prior to bloom and crop losses expressed as the proportion of diseased berries. For variables correlated with crop losses, a further objective was to assess whether it is possible to develop simple models that can predict raspberry yield losses prior to bloom, which correspond to the critical period for fungicide applications. This was done by evaluating the correlation pattern of weather and airborne inoculum variables with yield losses using windowpane analysis. The specific objectives were to determine the time-window lengths as well as the window start and end time relative to raspberry bloom, most highly correlated to yield losses; and, using the most correlated variable, to develop models for predicting yield losses.

MATERIALS AND METHODS

Description of sampling sites. The experiment was conducted from 2010 to 2012 in raspberry plantings on an Agriculture and Agri-Food Canada experimental farm and on a commercial farm, both located in the southeast region of the province of Quebec, Canada. In total, nine data sets were used in this study. On the experimental farm (S4 sites), data were collected in 2010, 2011, and 2012 in a plot measuring 30 by 20 m that had been planted in 2003 with raspberry cultivar Killarney. The rows were spaced 3.0 m apart, and the plants were spaced 75 cm apart within rows. On the commercial farm (S1, S2, and S3 sites), data were collected in 2010 and 2011, 2011 and 2012, and 2010 and 2011 for S1, S2, and S3, respectively. Data were collected in three plots, each measuring 30 by 50 m, located in a 2-ha planting established in 2005 with Killarney. The rows were spaced 3.0 m apart, and the plants were spaced 90 cm apart within rows. On both farms, raspberry were not managed for gray mold. Herbicides and insecticides were applied when needed.

Airborne *B. cinerea* conidia monitoring. On both farms, airborne conidium concentration was monitored using a 7-day volumetric spore sampler (Burkard Mfg. Co., Rickmansworth, UK). The sampler was placed in the center of the planting with the sampling

orifice at 0.6 m above the ground. The sampler was adjusted to sample air at 10 liters min⁻¹. Impaction tapes were coated with a thin layer of silicone grease (Dow Corning Co., Midland, MI) before placement in the sampler. The tapes were removed at 7-day intervals and then cut into 2-mm segments corresponding to 1-h periods. The number of conidia per 2 mm of tape was estimated using a previously developed quantitative polymerase chain reaction assay (Carisse et al. 2014). Conidia counts were converted to concentrations of conidia per cubic meter of air (Carisse et al. 2014).

Collection of weather data. On the experimental farm, data were obtained from an automatic weather station (CR-21X; Campbell Scientific Inc., Edmonton, AB, Canada) placed in the center of the plot. On the commercial farm, data were collected with WatchDog data loggers (Spectrum Technologies, Aurora, IL) placed in the center of the raspberry planting. Weather data were monitored every 15 min on the experimental farm and every 30 min on the commercial farm, and hourly averages were used in the analyses. Wetness sensors were placed within the raspberry canopy at the level of inflorescences, and temperature and RH probes were placed in a white shelter at 1.5 m above the ground. Rainfall was recorded with a tipping-bucket rain gauge (Geneq, Montreal, QC, Canada) at a height of 50 cm above the ground in an unobstructed area between the two central rows. Vapor pressure deficit (VPD) was derived from the listed values for water vapor pressure and temperature (Kaye and Laby 1957) and calculated as $VPD = Wvp[(1 - RH)/100]$ and $Wvp = 4.6698 \times e^{0.06241 \times T}$, where Wvp is water vapor pressure and T is temperature (°C). All weather variables were summarized over a day. Air temperature (°C), RH (%), solar radiation (kJ m⁻²), wind speed (km h⁻¹), and VPD (kPa) variables were expressed as averages: mean daily temperature (MDT), mean daily RH (MDRH), mean solar radiation (MSOLR), mean wind speed (MWS), and mean VPD (MVPD), respectively). Rainfall (RAIN) was expressed as accumulated values (in millimeters) and the wet period (WET) was defined as the number of hours (h) when the RH was above 90% or the raspberry leaves or flowers were wet. Bulger et al. (1987) studied the influence of temperature and wetness duration on flower infection and the subsequent proportion of fruit infected by *B. cinerea*. Their model was used to calculate a daily probability of infection (PI) on a scale of 0 to 100% (Bulger et al. 1987), as follows:

$$\ln[PI/(1-PI)] = -3.526 + (0.0228 \times WT) - (0.1949 \times T) - (0.000017 \times WT) \quad (1)$$

where W is the duration (in hours) of flower wetness and T is the temperature (°C) during the flower wetness period (Bulger et al. 1987). Weather and inoculum variables are presented in Table 1.

Collection of data on raspberry gray mold incidence and calculation of crop losses. For each of the nine site-years, 100 mature fruit were randomly picked from the two central rows on 10 plants per row. The fruit were placed in a plastic container so that the berries were not touching each other and then incubated for 2 days at 10°C. The incidence of diseased fruit was assessed based on the

TABLE 1. Description of weather- and inoculum-based variables used in windowpane analysis of *Botrytis* fruit rot of raspberry

Variables	Description (unit)
Daybloom	Number of days since bloom (10% flowering)
MDT	Mean daily temperature (°C)
MDRH	Mean daily relative humidity (%)
RAIN	Daily amount of rain (mm)
MVPD	Mean vapor pressure deficit (kPa)
WET	Daily number of wet hours (h)
PI	Probability of infection (%) (Broome et al. 1995)
MSOLR	Mean daily solar radiation (kJ m ⁻¹)
MWS	Mean daily wind speed (km h ⁻¹)
ACC	Number of airborne conidia m ⁻³
logACC+1	Log(number of airborne conidia m ⁻³ + 1)

presence of *B. cinerea* sporulation. This procedure was repeated for six harvests done over a 2-week period. Crop losses were expressed as the mean percentage of diseased berries over the six harvests.

Windowpane analysis. In order to measure the association between each weather variable and raspberry crop losses over time, windowpane analysis was used. The principle is to summarize the information available in a time window of defined length (in days) and starting time (Coakley et al. 1988; Goldwin 1982; Kriss et al. 2010). The window is meant to be moved sequentially along the time frame of data collection so that all observations are considered. Given a window length of m days, the first window starts at the last day of observation, and weather- or inoculum-based data are averaged on the basis of the subset of this specific day and the $m - 1$ previous days. The time window is then moved backward by 1-day increments, and the same process is repeated until the data frame has been entirely covered. The day of year (DOY) associated with the start of the growing season and the DOY associated with the end of the growing season varied from one year to another. In order to compare the data recorded in each year, a time scale referring to the day of bloom was used. For instance, weather and inoculum data were recorded at the two locations from day -17 to day 68 from bloom in 2010 and 2012 and from day -20 to day 64 from bloom in 2011.

Weather and inoculum data were exported to RStudio (v0.99.878) for further analyses (RStudio Team 2015). Nine new data frames (subsets) were created, one for each site-year of the sample, containing only weather and inoculum data for day -17 to day 64, to complete the standardization. Similarly, the crop loss data were imported in RStudio. Six data frames were then constructed for each harvest day. As a result, each table contained nine observations corresponding to the nine site-years studied. The seasonal mean of crop losses for each location was recorded in a new table.

The window lengths tested in this study ranged from 2 to 10 days. Because of the *B. cinerea* infection pathway, the short time period preceding bloom is most relevant for disease management decision making. Therefore, it was decided that a window should not exceed 10 days. To estimate the strength of the linear relationship between each summary weather or inoculum variable and crop losses for a given time window, the Pearson product-moment correlation coefficient was used because the response variable (percentage of diseased berries) was continuous. The Pearson correlation coefficient between a sample x and a sample y is defined as follows:

$$r = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{(n-1)s_x s_y} \quad (2)$$

TABLE 2. Window lengths, number of windows, and starting days used in windowpane analysis of Botrytis fruit rot of raspberry for the entire growing season^a

Length ^b	N ^c	Starting day (days from bloom) to end day (-17 from bloom) ^d
2	81	64, 63, ..., -15, -16
3	80	64, 63, ..., -14, -15
4	79	64, 63, ..., -13, -14
5	78	64, 63, ..., -12, -13
6	77	64, 63, ..., -11, -12
7	76	64, 63, ..., -10, -11
8	75	64, 63, ..., -9, -10
9	74	64, 63, ..., -8, -9
10	73	64, 63, ..., -7, -8

^a The time scale used in windowpane analysis is the number of days since bloom (10% flowering).

^b Length of the time window in days.

^c Number of windows that were fitted in the time frame, which decreases as the length increases.

^d Time windows began on day 64 and were moved backward by 1-day increments to day -17 from bloom. The last starting day of the sequence varied depending on the length of the window.

where r is the Pearson correlation coefficient, n is the sample size, $\bar{x}$ and $\bar{y}$ are the sample means of variables x and y , respectively, and s_x and s_y are the sample standard deviations of x and y , respectively. Several assumptions were made to meet the hypotheses underlying the use of this coefficient. First, it was assumed that there was a linear relationship between each summary weather or inoculum variable and crop losses. Also, the summarized variables for a given time window were assumed to be normally distributed. The Shapiro-Wilk test was run on the crop loss sample for each harvest day using the shapiro.test function in R (R Core Team 2016; Shapiro and Wilk 1965). The null hypothesis was never rejected at a level of $\alpha = 0.10$, leading us to accept that the response variable was normally distributed as well. The hypothesis of normality allowed us to test the significance of each correlation coefficient using the test statistic t , defined as follows:

$$t = r \cdot \sqrt{\frac{n-2}{1-r^2}} \quad (3)$$

This test statistic follows a Student distribution (Weisberg 2014). The validity of the resulting estimated correlation coefficients and corresponding P values relies on these assumptions.

A function was designed in R language to compute and record the Pearson correlation coefficient between each summary weather or inoculum variable and crop losses for each window length and start time. For a given time window of length m and start time d , each summary variable was determined by computing the mean of the daily values taken by the variable at each location over the course of those m days (day d to day $d - m + 1$). This way, $n = 9$ summary observations were obtained for each weather or inoculum variable. The coefficient of correlation between each summary variable and crop loss as well as its significance level were then computed with the cor and cor.test functions in R, respectively (R Core Team 2016). The calculation of the P value was done with a one-tailed test, assuming that the effect of any weather or inoculum variable on crop losses for a given time window was unidirectional (Kriss et al. 2010). After that, the time window was shifted from day d to day $d - 1$, and the latter process was repeated. This was done until the first day of the data frame (day -17) was included in a time window. Because there were 82 days of observations in each data frame, there were 81 windows of length 2, 80 windows of length 3, 79 windows of length 4, and so on (Table 2).

Following the path taken by Kriss et al. (2010), a second test was performed to minimize the number of false positives among the coefficients. The multiple hypothesis testing problem arises when the statistical significance of an intersection of null hypotheses needs to be assessed. In this case, for each weather or inoculum variable and each window length, numerous correlation coefficients were computed, because there are various starting times across the growing season. For instance, 81 correlation coefficients were computed along with their significance level with a 2-day window length for the 82-day time frame. If there is no regard for a particular coefficient, the event of observing at least one high or extreme value among them is likely to occur. At a given significance level α , the risk of incorrectly rejecting the null hypothesis (type I error) increases with increasing collections of hypotheses (Blakesley et al. 2009). A multiple hypothesis approach helps to prevent false positives. However, whereas the type I error is being controlled, the type II error, which is to falsely accept the null hypothesis, increases, leading to a reduced statistical power (Blakesley et al. 2009). Thus, the hypothesis that no correlation coefficient was significant was tested against the alternative, which is that at least one correlation coefficient was significant. However, the correlation coefficients were not independent. Two adjacent time windows differed only by 1 day of observations. The Simes method was used because it is appropriate for positively correlated tests (Sarkar and Chang 1997; Simes 1986). Let $P_1, P_2, \dots, P_n$ represent the P values corresponding to the collection of n test results, and let $P_{(1)}, P_{(2)}, \dots, P_{(n)}$ represent the ordered P values. Simes suggested rejecting the global null hypothesis at a critical threshold α if $P_{(j)} \leq (j \times \alpha)/n$ for any

j ($j = 1, \dots, n$). We can also adjust the ordered P values without changing the test, as follows:

$$\tilde{P}_j = \frac{n}{j} \cdot P_{(j)} \quad (4)$$

Given a window length and a weather or inoculum variable, the global P value P is the minimum of the $\tilde{P}_j$ value ($j = 1, \dots, n$). A correlation coefficient between a weather or inoculum variable and crop losses was declared significant for a specified window length if $P \leq \alpha$. A level of $\alpha = 0.05$ was chosen. The Simes test was performed on two different time frames, one including all 82 days of observations and the other ranging from day -17 to day 0 from bloom. The latter period was studied specifically for the purpose of constructing a model able to predict crop losses before the flowering period. Given that the global test result P is a function of the number of individual tests results, it was easier to achieve significance for a smaller time frame. In general, as the number of null hypotheses tested increases, for instance when the window length decreases, smaller individual P values are required for rejecting the global null hypothesis.

Also, for each weather or inoculum variable and window length, the highest coefficient of correlation was recorded along with its significance level for the two time frames discussed above. An individual coefficient was considered significant if its P value was < 0.005 , a level that makes it harder to reject the null hypothesis if the coefficient is actually 0; and that, therefore, reduces the number of false positives. However, as mentioned before for multiple-testing adjustment methods, such a small critical threshold can also lead to an increased number of false negatives. If we considered the entire time frame, in most cases, we observed that a significant global P value P led to a significant maximum correlation coefficient for any given weather- or inoculum-based variable and window length, as pointed out by Kriss et al. (2010).

Simple linear regression was used to describe the relationship between crop losses and significant 7-day average weather or inoculum variables for the prebloom time frame, including 7-day average airborne inoculum, 7-day average MDRH, 7-day average RAIN, and 7-day average WET, for starting days ranging from day -9

to day 1 from bloom. Univariate linear models were computed using the `lm()` function in R language (R Core Team 2016). Because it is expected that these variables interact together to influence crop losses, multiple linear regression was used to study the relationship between crop losses, 7-day average airborne inoculum, and the 7-day average of each of the humidity-related weather variables (MDRH, RAIN, and WET). The general form of the multiple linear models considered included two variables, as follows:

$$CL = \beta_0 + \beta_1 7DHUM_t + \beta_2 7DACC_t \quad (5)$$

where CL is the crop loss variable, $7DHUM_t$ is one of the 7-day average humidity-related variables (MDRH, RAIN, or WET) on starting day t , $7DACC_t$ is the 7-day average airborne conidia concentration on starting day t , β_0 is the intercept parameter, β_1 is the parameter corresponding to $7DHUM_t$, and β_2 is the parameter corresponding to $7DACC_t$. Starting times t both ranged from day -9 to day 1 from bloom but were not necessarily equal. Thus, there was a large set of possible models for each humidity-related variable considered. The best subsets automatic procedure was then used to find the starting days that provided the best-fitting models according to the coefficient of determination R^2 . This was done in R language using the `regsubsets()` function included in the `leaps` package (Lumley and Miller 2009; R Core Team 2016). Based on the output of the latter procedure, multiple linear models were computed through the `lm()` function of R (R Core Team 2016). For each model, the Pearson product-moment correlation coefficient between the two variables ($7DHUM_t$ and $7DACC_t$) was determined by using the `cor()` function in order to check for collinearity.

RESULTS

The average percentage of diseased berries varied from 8.0 to 62.2% (Fig. 1). In general, the percentage of diseased berries was higher on the experimental farm, with 54.0, 58.0, and 62.2% in 2012, 2011, and 2010, respectively (Fig. 1, S4). On the commercial farm, the percentage of diseased berries varied from 8 to 36.0%, depending on site and year (Fig. 1, S1, S2, and S3). Overall, for the period of 20 days before and after bloom, based on 7-day averages,

Fig. 1. Boxplots of crop losses (%) due to *Botrytis* fruit rot for nine site-years. There were six harvests at each location. The horizontal axis represents site-years. The vertical axis represents the percentage of diseased raspberry (crop losses). For each boxplot, the lower whisker cap represents the minimum value taken by the crop losses variable, and the higher whisker cap represents the maximum. From bottom to top, except for the thicker line and whisker caps, each horizontal line marks 25, 50, and 75% of data points, respectively. The thick horizontal line is the mean crop losses of the site-year. When the median (line marking 50% of data points) is not visible, it means that it is equal or almost equal to the mean and that the distribution is approximately symmetrical.

there was a similar temporal trend for most of the weather variables (Fig. 2). However, the magnitudes of the values differ for the different sites and years (Fig. 2).

To better visualize the correlation between crop losses and weather- or inoculum-based variables, correlograms were prepared

(Figs. 3, 4, and 5). These correlograms were built from Pearson correlation coefficients between each of the weather- or inoculum-based variables and mean crop losses and for 3-, 5-, 7-, and 9-day windows during the period of 17 days before bloom (day -17) to 64 days after bloom (day 64). For all weather- and inoculum-based

Fig. 2. Weather and airborne conidia concentration variables expressed as 7-day moving averages for nine site-years. The horizontal axes represent the starting time of the 7-day windows. Each line corresponds to one site-year, as described in the legend. Each value of the dependent variable is an average based on the starting day and the previous 6 days of observations. The time scale used is the number of days since bloom (10% flowering). MDT = mean daily temperature, MDRH = mean daily relative humidity, RAIN = daily amount of rainfall, MVPD = mean vapor pressure deficit, WET = number of wet hours, MSOLR = mean solar radiation, MWS = mean wind speed, and ACC = airborne conidia concentration.

variables, large fluctuations in correlation coefficients were observed for 3-day windows, and fluctuation diminished as the length of the window increased (Figs. 3, 4, and 5). For MDT, during the period preceding bloom and regardless of the window length, the correlation coefficients were below the significance level of $\alpha = 0.05$

(Fig. 3). For MDRH, for 5-, 7-, and 9-day windows and before bloom, most correlation coefficients were between the significance levels of $\alpha = 0.05$ and $\alpha = 0.005$ (Fig. 3). For RAIN and during the period preceding bloom, most correlation coefficients were below the significance level of $\alpha = 0.05$ when the lengths of windows were

Fig. 3. Pearson product-moment correlation coefficients for the relationships between mean daily temperature (MDT) ($^{\circ}\text{C}$), mean daily relative humidity (MDRH) (%), or daily amount of rainfall (RAIN) (mm) and crop losses due to Botrytis fruit rot (%). Window lengths of 3, 5, 7, and 9 days are shown for each environmental variable. Horizontal axes represent the starting time of the window of defined length, which is expressed as the number of days since bloom. The dotted horizontal line is at the critical correlation coefficient for individual significance of $\alpha = 0.005$ on the basis of a one-sided test, and the dash-dot-dot horizontal line marks a significance level of $\alpha = 0.05$.

3 and 5 days (Fig. 3). However, for windows of 7 and 9 days, several coefficients were between the significance levels of $\alpha = 0.05$ and $\alpha = 0.005$ (Fig. 3). For MVPD, the Pearson correlation coefficients were negative and mostly not significant during the prebloom period (Fig. 4). For both WET and PI, when the window lengths were greater than 5 days, most correlation coefficients were between

the significance levels of $\alpha = 0.05$ and $\alpha = 0.005$ (Fig. 4). For MSOLR and MWS, regardless of the window length, most correlation coefficients were negative and below the significance level of $\alpha = 0.05$ (Fig. 5). Finally, for airborne conidia concentration (ACC), there was a large variation in correlation coefficients for windows of 3 and 5 days; however, for windows of 7 and 9 days, most

Fig. 4. Pearson product-moment correlation coefficients for the relationships between mean daily vapor pressure deficit (MVPD) (kPa), number of wet hours (WET), or probability of infection (PI) and crop losses due to Botrytis fruit rot (%). Window lengths of 3, 5, 7, and 9 days are shown for each variable. Horizontal axes represent the starting time of the window of defined length, which is expressed as the number of days since bloom. The dotted horizontal line is at the critical correlation coefficient for individual significance of $\alpha = 0.005$ on the basis of a one-sided test, and the dash-dot-dot horizontal line marks a significance level of $\alpha = 0.05$.

coefficients were between the level of significance of $\alpha = 0.05$ and $\alpha = 0.005$ (Fig. 5).

Because of the difficulty of determining the best window length based only on the inspection of correlograms, the Simes-adjusted P values and maximum Pearson correlation coefficient were calculated

for window lengths of 2 to 10 days (Tables 3 and 4). For the period of 17 days before bloom to 64 days after bloom, regardless of the window length, based on the Simes-adjusted P values, there were significant correlations between crop losses and MDT, crop losses and MDRH, crop losses and RAIN, crop losses and WET, and crop

Fig. 5. Pearson product-moment correlation coefficients for the relationships between mean daily solar radiation (MSOLR) (kJ m^{-2}), mean daily wind speed (MWS) (km h^{-1}), or airborne conidia concentration (ACC) (number of conidia m^{-3}) and crop losses due to Botrytis fruit rot (%). Window lengths of 3, 5, 7, and 9 days are shown for each variable. Horizontal axes represent the starting time of the window of defined length, which is expressed as the number of days since bloom. The dotted horizontal line is at the critical correlation coefficient for individual significance of $\alpha = 0.005$ on the basis of a one-sided test, and the dash-dot horizontal line marks a significance level of $\alpha = 0.05$.

TABLE 3. Adjusted significance levels based on the Simes method and maximum Pearson correlation coefficients between crop losses due to *Botrytis cinerea* and weather or inoculum variables for specified window lengths when the entire time frame was considered, based on nine site-years of data^a

Variable ^b	Significance level for window length (days)								
	2	3	4	5	6	7	8	9	10
<i>P</i> ^c									
MDT	0.105	0.073	0.048	0.037	0.040	0.038	0.033	0.033	0.028
MDRH	0.048	0.035	0.037	0.033	0.035	0.035	0.036	0.031	0.030
RAIN	0.194	0.155	0.107	0.084	0.055	0.043	0.039	0.046	0.039
MVPD	0.240	0.191	0.175	0.159	0.174	0.160	0.144	0.143	0.147
WET	0.140	0.075	0.067	0.059	0.041	0.044	0.049	0.048	0.040
PI	0.058	0.071	0.083	0.085	0.079	0.079	0.080	0.082	0.079
MSOLR	0.401	0.367	0.326	0.295	0.255	0.244	0.235	0.208	0.189
MWS	0.443	0.389	0.405	0.393	0.423	0.418	0.433	0.440	0.437
ACC	0.114	0.099	0.085	0.077	0.071	0.034	0.015	0.010	0.006
logACC	0.034	0.035	0.031	0.029	0.027	0.026	0.023	0.018	0.016
Pearson ^d									
MDT	0.817	0.848	0.828	0.845	0.847	0.829	0.830	0.845	0.832
MDRH	0.859	0.843	0.873	0.838	0.819	0.839	0.820	0.819	0.806
RAIN	0.836	0.830	0.812	0.812	0.842	0.865	0.844	0.843	0.873
MVPD	-0.827	-0.795	-0.785	-0.770	-0.798	-0.783	-0.743	-0.736	-0.709
WET	0.833	0.861	0.855	0.877	0.860	0.876	0.864	0.878	0.876
PI	0.885	0.833	0.814	0.752	0.749	0.741	0.755	0.759	0.718
MSOLR	-0.779	-0.644	-0.678	-0.630	-0.641	-0.638	-0.646	-0.633	-0.653
MWS	-0.705	-0.704	-0.630	-0.644	-0.593	-0.553	-0.547	-0.572	-0.626
ACC	0.856	0.853	0.814	0.838	0.875	0.880	0.905	0.926	0.928
logACC	0.851	0.842	0.898	0.843	0.850	0.855	0.875	0.876	0.874

^a The time frame considered ranged from day -17 from bloom to day 64 from bloom.

^b MDT = mean daily temperature (°C), MDRH = mean daily relative humidity (%), RAIN = daily amount of rain (mm), MVPD = mean vapor pressure deficit (kPa), WET = daily number of wet hours (h), PI = probability of infection (%), MSOLR = mean daily solar radiation (kJ m⁻¹), MWS = mean daily wind speed (km h⁻¹), ACC = number of airborne conidia m⁻³, and logACC+1 = log(Number of airborne conidia m⁻³ + 1).

^c Correction for multiple correlated statistics. *P* is the global *P* value obtained after the Simes method was used for a collection of time windows of specified window length. The null hypothesis was rejected for values of *P* < 0.05.

^d Maximum Pearson correlation coefficient for a collection of time windows of specified window length. Individual correlation coefficients higher than 0.582 were significant at $\alpha = 0.05$; those higher than 0.798 were significant at $\alpha = 0.005$. Correlation coefficients in bold are significant at $\alpha = 0.005$.

TABLE 4. Adjusted significance levels based on the Simes method and maximum Pearson correlation coefficients found between crop losses due to *Botrytis cinerea* and environmental factors for specified window lengths when the prebloom time frame is considered, based on nine site-years of data^a

Variable ^b	Significance level for window length (days)								
	2	3	4	5	6	7	8	9	10
<i>P</i> ^c									
MDT	0.110	0.117	0.086	0.080	0.100	0.107	0.115	0.126	0.106
MDRH	0.020	0.025	0.030	0.020	0.015	0.018	0.020	0.016	0.013
RAIN	0.043	0.045	0.058	0.039	0.035	0.016	0.011	0.019	0.010
MVPD	0.173	0.079	0.098	0.090	0.079	0.077	0.064	0.058	0.049
WET	0.045	0.023	0.017	0.019	0.018	0.012	0.013	0.009	0.008
PI	0.021	0.032	0.041	0.043	0.041	0.036	0.035	0.037	0.034
MSOLR	0.114	0.293	0.280	0.281	0.165	0.196	0.084	0.090	0.088
MWS	0.384	0.273	0.288	0.304	0.354	0.380	0.393	0.420	0.412
ACC	0.116	0.104	0.098	0.055	0.030	0.011	0.004	0.002	0.001
logACC	0.045	0.088	0.048	0.037	0.024	0.011	0.009	0.006	0.005
Pearson ^d									
MDT	0.762	0.730	0.715	0.734	0.729	0.646	0.645	0.627	0.606
MDRH	0.859	0.828	0.801	0.795	0.794	0.839	0.818	0.779	0.786
RAIN	0.836	0.830	0.790	0.792	0.810	0.827	0.843	0.843	0.873
MVPD	-0.730	-0.763	-0.712	-0.725	-0.707	-0.706	-0.646	-0.680	-0.676
WET	0.833	0.861	0.855	0.825	0.860	0.876	0.864	0.878	0.876
PI	0.861	0.799	0.787	0.748	0.749	0.741	0.743	0.732	0.718
MSOLR	-0.779	-0.532	-0.584	-0.630	-0.607	-0.604	-0.646	-0.633	-0.653
MWS	0.440	-0.704	-0.439	-0.488	-0.503	-0.418	0.286	0.267	0.271
ACC	0.689	0.702	0.762	0.812	0.816	0.879	0.905	0.926	0.928
logACC	0.833	0.755	0.823	0.833	0.850	0.855	0.875	0.876	0.869

^a The time frame considered ranged from day -17 from bloom to day 0 from bloom.

^b MDT = mean daily temperature (°C), MDRH = mean daily relative humidity (%), RAIN = daily amount of rain (mm), MVPD = mean vapor pressure deficit (kPa), WET = daily number of wet hours (h), PI = probability of infection (%), MSOLR = mean daily solar radiation (kJ m⁻¹), MWS = mean daily wind speed (km h⁻¹), ACC = number of airborne conidia m⁻³, and logACC+1 = log(Number of airborne conidia m⁻³ + 1).

^c Correction for multiple correlated statistics. *P* is the global *P* value obtained after the Simes method was used for a collection of time windows of specified window length. The null hypothesis is rejected for values of *P* < 0.05.

^d Maximum Pearson correlation coefficient for a collection of time windows of specified window length. Individual correlation coefficients higher than 0.582 were significant at $\alpha = 0.05$; those higher than 0.798 were significant at $\alpha = 0.005$. Correlation coefficients in bold are significant at $\alpha = 0.005$.

losses and ACC (Table 3). Correlations between crop losses and MVPD and between crop losses and PI were significant only for window lengths of 2 and 6 days and 2, 3, and 4 days, respectively (Table 3). However, for the period preceding bloom only, and based on the Simes-adjusted P values, there was a significant correlation between crop losses and MDRH (window lengths of 2 to 4 days and 7 to 10 days), crop losses and RAIN (window lengths of 2 to 3 days and 6 to 10 days), crop losses and WET duration, and crop losses and ACC (window length of 5 to 10 days) (Table 4).

Significant (according to P values) windows and weather or inoculum variables with the highest correlation for the prebloom time frame were further analyzed to identify short periods for which there was a strong correlation between a weather or inoculum variable and crop losses. There was no formal statistical method used for the model selection. As Kriss et al. (2010) did, variables and time windows for which there was a cluster of at least three significant correlation coefficients at a level of 0.05 around the maximum coefficient observed were selected. This criterion was

met mostly by longer window lengths. Based on the correlograms and Simes-adjusted P values, window lengths of 7 days for MDRH, RAIN, WET, and ACC were selected as the best indicators of crop losses (Fig. 6). The relationships between crop losses and 7-day averages for these variables for 8, 6, 4, and 2 days before bloom are presented in Figure 6. Overall, the coefficients of determination varied from $R^2 = 0.25$ to $R^2 = 0.77$. However, when crop losses were modeled based on 7-day average airborne inoculum and 7-day averages of each of the humidity-related weather variables (MDRH, RAIN, and WET), the coefficients of determination ranged from $R^2 = 0.83$ to $R^2 = 0.89$ (Fig. 7; Table 5).

DISCUSSION

In Canada, most raspberry plants are grown in open fields, and controlling BFR has been an ongoing, multifaceted challenge: there are several sources of primary inoculum within and outside raspberry plantings, and the pathogen produces large amounts of

Fig. 6. Relationships between raspberry seasonal crop losses caused by *Botrytis cinerea* and significantly correlated weather or inoculum variables expressed as 7-day averages for days -8, -6, -4, -2, and 0 from bloom. Data were collected in nine site-years. Horizontal axes represent weather variables averaged over the specified starting day and the previous 6 days. For each scatterplot, a regression was computed and a trend line was added to the graph.

secondary inoculum. The disease can severely reduce fruit quality, marketable crop yield, and storability even with fungicide use. *B. cinerea* infects not only flowers and fruit but also primocanes, causing lesions and wilt (Botrytis cane blight), which reduce plant vigor. In all production regions, resistance to several fungicides registered for Botrytis diseases control was reported (Gossen et al. 2014). The quiescent nature of the flower infections makes monitoring the disease impossible. Finally, near or during the harvest period, the application of fungicide is complicated by the preharvest delay required by the legislation on fungicide use.

In raspberry production, the two *B. cinerea* infection pathways (Dashwood and Fox 1988)—the establishment of quiescent mycelium in floral parts and berry-to-berry infections—mean that the control of fruit rot relies mostly on applications of fungicides during the flowering and early fruiting periods. In the absence of disease risk indicators, growers tend to apply fungicides on the basis of the phenological stage of the raspberry crop, regardless of the weather conditions. This approach results in only three to four fungicide applications annually. However, the increasing incidence of fungicide-resistant individuals in *B. cinerea* populations, the removal of fungicides from the list of fungicides registered for Botrytis disease control, and the

exposure of pollinators to fungicides during bloom support the need for improved use of fungicides. In eastern Canada, most raspberry crops are marketed as pick-your-own on the farm or as direct retail on the farm or at farm markets. To maintain a constant supply during the raspberry season, growers often need to keep harvested berries in cold storage for few days. Hence, knowing in advance the potential for losses due to *B. cinerea* is crucial to enable growers to determine optimal storage times and marketing strategies.

Considering the importance of Botrytis diseases in berry crops (Carisse 2016), prediction models were developed to estimate the risk of infection from mostly temperature and duration of wetness or humid periods (Broome et al. 1995; Bulger et al. 1987; Nair and Allen 1993). These models were not developed for raspberry and, in general, were not validated against field data. Because of the importance of airborne inoculum during the flower infection period and, to a lesser extent, during fruit ripening and harvest, failing to consider inoculum in prediction models for Botrytis-induced diseases may affect model prediction ability (accuracy) (Blanco et al. 2006; Carisse et al. 2014; Jarvis 1962a). Xu et al. (2000) showed that including airborne inoculum in a weather-based model for strawberry infection by *B. cinerea* improved accuracy.

Fig. 7. Contour plots displaying the relationships between raspberry seasonal crop losses due to *Botrytis cinerea* and different pairs of weather or inoculum variables expressed as 7-day averages. Data were collected in nine site-years. Each environmental variable was averaged over the specified day and the preceding 6 days. Vertical axes represent 7-day average airborne inoculum concentration (ACC) 7 days before the flowering period. The horizontal axis on the left represents 7-day average mean daily relative humidity (MDRH) (%) on day -7 from bloom, the horizontal axis in the middle represents 7-day average number of wet hours (WET) on day -8 from bloom, and the horizontal axis on the right represents 7-day average rainfall (RAIN) (mm) on day 0 from bloom. Each solid line is a contour line representing a level of yield losses (%) by intervals of 10. Dotted contour lines mark levels of yield losses (%) by intervals of 2.

TABLE 5. Statistics of multiple linear regression of the relationships between crop losses caused by *Botrytis cinerea* and 7-day average airborne inoculum and 7-day averages of each of the humidity-related weather variables for various time periods preceding bloom

Model ^a	β_0^b	β_1^b	β_2^b	R^2	MSE ^c	r^d
7DMDRH ₋₇ + 7DACC ₋₇	-157.210 (62.28)	2.251 (0.88)	0.200 (0.06)	0.89	7.62	0.66
7DMDRH ₋₈ + 7DACC ₋₇	-108.251 (47.04)	1.539 (0.65)	0.242 (0.06)	0.88	7.95	0.48
7DMDRH ₋₆ + 7DACC ₋₇	-106.623 (48.25)	1.624 (0.72)	0.229 (0.06)	0.88	8.10	0.56
7DMDRH ₋₈ + 7DACC ₋₈	-148.539 (46.11)	2.126 (0.62)	0.202 (0.05)	0.87	8.25	0.30
7DMDRH ₋₆ + 7DACC ₋₈	-143.057 (47.61)	2.197 (0.69)	0.185 (0.05)	0.86	8.62	0.40
7DMDRH ₋₅ + 7DACC ₋₇	-81.496 (44.53)	1.290 (0.68)	0.238 (0.06)	0.86	8.73	0.55
7DWET ₋₇ + 7DACC ₋₆	-5.861 (7.44)	2.444 (0.81)	0.230 (0.06)	0.85	8.91	0.34
7DMDRH ₋₉ + 7DACC ₋₈	-94.096 (34.21)	1.376 (0.46)	0.226 (0.05)	0.85	8.91	0.17
7DWET ₋₈ + 7DACC ₋₇	-6.260 (7.99)	2.795 (1.60)	0.170 (0.09)	0.85	8.98	0.81
7DRAIN ₀ + 7DACC ₋₇	-5.785 (8.10)	0.211 (0.08)	3.543 (2.15)	0.84	9.15	0.71
7DRAIN ₁ + 7DACC ₋₇	-5.025 (7.94)	0.219 (0.08)	3.373 (2.10)	0.84	9.22	0.69
7DRAIN ₋₁ + 7DACC ₋₇	-6.279 (8.86)	0.205 (0.09)	3.184 (2.19)	0.83	9.49	0.76

^a 7D stands for 7-day average. MDRH, RAIN, WET, and ACC are mean daily relative humidity, rain, wetness duration, and airborne conidia concentration, respectively. The subscript represents the last day of the 7-day window.

^b Parameters: β_0 is the intercept parameter of the regression, β_1 is the coefficient parameter associated with a humidity-related variable (MDRH, RAIN, or WET), and β_2 is the coefficient parameter associated with airborne conidia concentration (ACC).

^c Mean standard error.

^d Pearson product-moment correlation coefficient between the covariates of the model.

In botanical epidemiology, two main approaches are used to relate weather to disease development. One approach consists of using all available knowledge on interactions between weather, pathogen, and host factors and on various phases of disease development to build a model that mimic disease progress. This approach was successfully used by González-Domínguez et al. (2015) to simulate *Botrytis* bunch rot of grape. Another approach, which assumes that knowledge of the factors that affect disease development is not complete, consists of exploring a range of variables occurring during a range of time periods varying in both length and starting date (Goldwin 1982). In the present study, our premise was that the available knowledge concerning BFR in raspberry is not sufficient to build simulation models and that weather factors and inoculum concentration somehow affect BFR in raspberry.

Consequently, an empirical approach (windowpane analysis) was taken to develop risk indicators for BFR due to *B. cinerea*, expressed as the percentage of diseased berries, on the basis of weather and inoculum variables. Windowpane analysis was used by a few epidemiologists to identify critical periods and weather variables that affect disease development (Coakley et al. 1985, 1988; Kriss et al. 2010). Coakley et al. (1985) initially used windowpane analysis to identify weather variables associated with the severity of Septoria leaf blotch of winter wheat caused by *Mycosphaerella graminicola* and to develop disease severity prediction models. Later, windowpane analysis was used to develop prediction models for stripe rust of winter wheat caused by *Puccinia striiformis* (Coakley et al. 1988).

The long-term objective of this study was to develop simple, reliable yield loss indicators that can be calculated 1 to 2 weeks before flowering in order to help with timing fungicide applications and the harvest schedule and with determining the best storage duration. This study represents an initial step toward identifying the weather- and inoculum-based variables most correlated with BFR in raspberry and determining the time-window length and starting time when these variables are most highly correlated with yield losses. In other words, the aim was to detect potential critical periods where one or more weather or inoculum variables have a pivotal impact on raspberry crop losses. Windowpane analysis was used to determine whether any such critical period exists and to specify the beginning and duration of this period. When the entire season was considered, most variables showed significant correlations with crop losses at all or some window lengths from 2 to 10 days. Regardless of the window length, the daily wind speed and solar radiation were not significantly correlated with crop losses, and the PI calculated from temperature and wetness duration was significantly correlated with crop losses only for a short window length of 2 to 4 days (Table 4). When only the period preceding bloom was considered, only humidity-related variables and airborne inoculum were correlated with crop losses for most window lengths (Table 4). The selection of the best window length is somewhat subjective. The window length should be characterized by high correlation coefficients; however, a short window may include high correlation coefficients owing to chance. In contrast, a too-long window may be difficult to interpret and will reduce the “prediction time,” because the period should be completed before averages are calculated. Based on both windowpane analysis and practicability, a window length of 7 days was selected. Using 7-day average airborne inoculum concentration combined with 7-day average RH for periods ending 6 to 8 days before bloom, it was possible to predict crop losses accurately (R^2 of 0.86 to 0.89).

In conclusion, there was no evidence in this study, regardless of the time-window length, of correlations between crop losses and temperature, VPD, wind, solar radiation, or PI. However, there was a significant correlation between crop losses and airborne inoculum and between crop losses and humidity-related variables, and the best window length was identified as 7 days. These findings are in accordance with field observations by Jarvis (1964), who reported

that high rainfall and long periods of high RH occurring 30 days before the first harvest were correlated with high incidence of gray mold on strawberry caused by *B. cinerea*. Similar correlations were not found for raspberry but correlations between humidity-related variables were found for various periods of time preceding picking (Jarvis 1964). In this study, windowpane analysis allowed a more formal selection of variables and of the length of critical periods. The results of this study can serve as a foundation to develop tools based on humidity and airborne inoculum monitoring to help manage raspberry fruit rot and to optimize harvesting and storage operations.

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