

Development of grape downy mildew (Plasmopara viticola) under northern viticulture conditions: influence of fall disease incidence

Odile Carisse

Accepted: 31 August 2015 /Published online: 15 October 2015 \odot Koninklijke Nederlandse Planteziektenkundige Vereniging 2015

Abstract In Eastern Canada, several of the grape (Vitis spp.) cultivars susceptible to downy mildew (Plasmopara viticola) are hybrids (e.g. 'Chancellor' and 'Vidal') that are protected with soil or geotextile fabric during the winter months. This practice, although useful for protecting vines from winter injuries, provides shelter for P. viticola oospores during adverse winter conditions. It is thus expected that a large proportion of P. viticola oospores will overwinter. The objective of this study was to investigate the relationship between fall downy mildew incidence and disease development in the following spring. This relationship was established using data collected from 2008 to 2011 in plantings with the cultivars 'Chancellor', 'Vidal', and 'Seyval Blanc' in plots with fall mildew incidence of 0 % to 2.5 %, >2.5 % to 5 %, >5 % to 10 %, and >10 % to 20 %. Downy mildew severity was assessed weekly from bud break until harvest, and the proportion of leaf area diseased at 25 % bloom and at harvest, the area under the disease progress curve, the time to 50 % maximum disease, the rate of disease progress, and the yield were estimated. Regardless of the cultivar and year, fall mildew incidence had a significant effect on mildew progress. Higher fall mildew incidence was associated with earlier development of symptoms and

O. Carisse (\boxtimes)

Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Gouin Boulevard, Saint-Jean-sur-Richelieu, QC J3B 3E6, Canada e-mail: odile.carisse@agr.gc.ca

higher severity of mildew at bloom in the following spring. This information could be used to determine the most appropriate strategy to manage downy mildew during the following spring. However, more research is needed to determine how management strategies should be adapted to the various levels of risk.

Keywords Disease carry over. Grape disease management . IPM . Epidemiology

Introduction

Wine is a leading product for agro-tourism in Eastern Canada, where small vineyards are located along various wine routes. Growing grapes (Vitis spp.) in a cold climate is challenging, because the grape varieties grown must produce mature grapes within the frost-free period, make good wine, and survive the winter conditions, particularly temperatures below −30 °C. Hence, cultivars such as 'Chancellor', 'Vidal', or 'Seyval Blanc' must be protected during the winter months because they are injured at temperatures below −25 °C (Jolivet and Dubois [2000](#page-9-0)). There are two main methods of winter protection: the vines can be covered either with geotextiles fabric or with soil from between the rows. In both cases, the objective is to keep the temperature around the vines above −15 °C (Jolivet and Dubois [2000\)](#page-9-0).

Downy mildew is one of the most important grape diseases worldwide. It is caused by Plasmopara

viticola, which was first observed in 1834 in the northeastern USA, its centre of origin (Gessler et al. [2011\)](#page-9-0). Because of the importance of this crop and of this disease, many scientific and technical reports are available on P. viticola ecology and downy mildew epidemiology and management (Gessler et al. [2011](#page-9-0)). In their review, Gessler et al. [\(2011\)](#page-9-0) mention that since 1910, more than 3000 reports had been published on grape downy mildew.

Grape downy mildew is a polycyclic disease with two distinct phases, namely the primary infections caused by oospores and the secondary infections caused by sporangia. The life cycle of P. viticola and the epidemiology of grape downy mildew are well known and documented (Gessler et al. [2011](#page-9-0)). In brief, P. viticola overwinters as oospores within infected leaves on the soil surface or within the surface layer of the soil. Oospore production in the fall is favored by dry conditions and occurs under a wide range of temperatures during leaf senescence (Rouzet and Jacquin [2003\)](#page-10-0). Depending on cultivar susceptibility and mildew severity during the growing season, up to 50,000 oospores can be produced per square meter of vineyard floor (Rossi et al. [2008b](#page-9-0); Rossi et al. [2009](#page-10-0)). These oospores mature during the late winter and early spring, and mature oospores germinate during the spring, causing the primary infections. Oospore maturation occurs in two distinct phases: first, oospores mature morphologically, resulting in the thinning of their outer membrane, and then they mature physiologically, a phase that corresponds to a reorganization of the nucleic material and lipid reserves (Vercesi et al. [1999](#page-10-0)). In the spring, the germination of mature oospores is favored by the rupture of their outer wall, which might be caused by a minor frost. The temperature influences the time at which primary infections begin. The germination of oospores starts when the soil temperature reaches 12 °C and the soil is wet; an accumulation of 160° days (base temperature of 8 °C) is necessary to break oospore dormancy (Rouzet and Jacquin [2003\)](#page-10-0). Once dormancy has been broken, germination is influenced by temperature, rain, and humidity (Caffi et al. [2009](#page-9-0); Hill [2000;](#page-9-0) Rossi et al. [2008a,](#page-9-0) [2008b\)](#page-9-0). Oospore germination is favored by temperatures above 11 \degree C (Park et al. [1997](#page-9-0)) and inhibited by temperatures above 30 °C (Blouin [2007](#page-9-0)). In

Eastern Canada, the favorable period for oospore germination corresponds to May to June. However, the germination of oospores may occur over a period of 2 to 3 months (Gobbin et al. [2003,](#page-9-0) [2005](#page-9-0)). Under favorable conditions, up to 50 zoospores per oospore could be produced and rainsplashed to new shoots or bunches located near the ground (Rossi and Caffi [2012;](#page-9-0) Viret and Siegfried [1996](#page-10-0)). Vines that require winter protection are usually trained so that fruiting buds are located at a maximum of 30 to 40 cm from the ground (Low Head system), making them highly vulnerable to infection by splashed zoospores.

The first symptoms of downy mildew infection typically appear at the time of emergence of inflorescences. However, on winter-protected vines and under severe disease pressure, symptoms on newly emerging shoots may appear soon after soil removal in the spring, which coincides with the bud break period (Fig. [1\)](#page-2-0). Zoospores that fall on susceptible tissues encyst in healthy tissues (Kiefer et al. [2002\)](#page-9-0) and infect the vines, provided that the tissue wetness, temperature, and ontogenic resistance conditions are favorable (Kennelly et al. [2005](#page-9-0); Lalancette et al. [1987;](#page-9-0) Riemann et al. [2002](#page-9-0)). The incubation period varies from 4 to 9 days depending on air temperature, relative humidity, and vine susceptibility (Kennelly et al. [2007;](#page-9-0) Orlandini et al. [2008;](#page-9-0) Rosa et al. [1995\)](#page-9-0). Lesions first appear as oil spots and progress to become reddish brown. Sporangia are produced on the underside of leaf lesions, on infected tendrils, and on berries. These sporangia will act as secondary inoculum.

Most damage is caused by infections of inflorescences, which result in flower rot, and by infections of bunches before the nouaison growth stage. Later infections are less likely to cause direct losses because the berries are less susceptible once the veraison stage has been reached (Kennelly et al. [2005\)](#page-9-0). Consequently, from a yield standpoint, early infections are much more damaging than are late infections (after nouaison) (Galet [1977](#page-9-0); Jermini et al. [2010](#page-9-0)). Downy mildew affects the quantity and quality of the berries produced. In addition, late infections reduce vine vigor (Davidou and Crachereau [2011](#page-9-0); Dubos [2002\)](#page-9-0). This latter consequence is especially important for northern viticulture, because the vines must be

Fig. 1 Downy mildew symptoms caused by *Plasmopara viticola* on newly emerged shoot (a) and on clusters located near the ground (b)

vigorous enough in the fall to survive during the winter months.

Because of the polycyclic nature of the disease and the importance of oospores as initial inoculum, the management of grape downy mildew generally relies on fungicide applications early in the season to control primary infections and to avoid infections of inflorescences, flowers, and young berries. Considering that the most important weather factor affecting oospore survival is temperature (Galet [1977](#page-9-0)), one can hypothesize that the methods of protecting vines for the winter favor the winter survival of oospores. If that is the case, the amount of mildew on leaves in the fall should influence the onset and severity of mildew in the following season. However, the nature of this relationship is unknown. The objective of this study was to examine the influence of downy mildew incidence in the fall on disease onset, disease progress, and yield reduction in the following season on vines that are protected for the winter.

Materials and methods

Vineyard description

The experiments were conducted at the Agriculture and Agri-Food Canada experimental farm located in Frelighsburg, Quebec, Canada (lat. 45°03′12″ N, long. 72°51′42″ W). The experiments were conducted from 2008 to 2011 in vineyards planted in 2003. A first set of data was collected in an experimental vineyard planted with Chancellor, a cultivar highly susceptible to downy mildew. A total of 16 subplots, each measuring 12×12 m, were arranged in a Latin square with each subplot 6 m away from another one and were used to test the influence of fall downy mildew incidence on disease development in the following season. In the fall of 2008, 2009, and 2010, all the subplots were assessed during the last week of September for leaf downy mildew incidence. At each assessment, the 15 youngest leaves on two shoots from eight vines per subplot were examined for the presence or absence of downy mildew. Downy mildew incidence was defined as the percentage of mildewed leaves. The subplots were then grouped based on downy mildew incidence into four groups corresponding to incidences of 0 % to 2.5 %, >2.5 % to 5 %, >5 % to 10 %, and >10 % to 20 % diseased leaves. From each incidence group, three subplots were selected. Hence, of the 16 subplots, 12 were used each year (four mildew incidences \times three replicates). Because downy mildew incidence increased over the years, the subplots with more than 25 % downy mildew incidence were managed in the following season to keep downy mildew incidence within the selected incidence categories. The second set of data was collected in control plots of downy mildew management trials performed in replicated experimental plots measuring 12×12 m and planted with Vidal, a susceptible cultivar, and Seyval Blanc, a moderately susceptible cultivar. In the fall of 2008, 2009, and 2010, all the experimental plots were assessed for leaf downy mildew incidence as described above. Each year, three plots with fall

downy mildew incidence within each of the previously described categories were selected.

For winter protection, the lower parts of the plants were covered, in the fall after leaf drop, with 40 to 60 cm of soil, which was removed in the following spring. During the 3 years of the study, insecticides were applied when required, mainly to control flea beetle (Altica chalybea). Fungicides were applied to control both powdery mildew (Erysiphe necator) and Botrytis bunch rot (Botrytis cinerea). Other cultural practices were done in accordance with the standard practices used in the other parts of the vineyard (Ontario Ministry of Agriculture, Food and Rural Affairs [2008](#page-9-0)).

Data collection

Grape downy mildew was assessed weekly from bud break (mid-May) until harvest (late September to early October) by looking at two shoots on the same eight vines, selected randomly at the first sampling. At each sampling, the total number of leaves and the percent leaf area diseased were recorded. The percent leaf area diseased was estimated using a scale that was divided into eight classes corresponding to 0 $\%$, >0 % to 1 $\%$, >1 % to 5 %, >5 % to 10 %, >10 % to 20 %, >20 % to 40 %, >40 % to 80 %, and >80 % to 100 % leaf area diseased. The yield was estimated based on the total weight in kilograms of marketable clusters per vine.

Data analysis A first set of variables was derived directly from the data collected, namely the percent leaf area diseased at 25 $\%$ bloom (PLAD $_{\text{bloom}}$) and at harvest (PLADharvest), the yield at harvest, and the area under the disease progress curve standardized for the epidemic duration ($AUDPC_{std}$), using the following equation:

$$
AUDPC = \sum_{i}^{n-1} \left(\frac{PLAD_i + PLAD_{i+1}}{2} \right) \times (t_{i+1} - t_i)
$$

where *n* is the number of assessments, and $PLAD_i$ is the percent leaf area diseased at time t_i .

Another set of parameters was derived from fitting a growth model to the percent leaf area diseased data expressed as a proportion of maximum cumulative percent leaf area diseased (PCPLAD), so that the data ranged from 0 to 1. Based on the observed patterns of PCPLAD progress, the sigmoid model (Eq. 2) was fitted to the data as follows:

$$
PCPLAD = \frac{1}{1 + e^{\left(\frac{-(x-x_0)}{b}\right)}}
$$

where x is the time in days of the year, x_0 is the time at which the PCPLAD is one half of the maximum, and b is the slope of the linear portion of the sigmoid curve.

Curve fitting was done separately for each cultivar and each year. Non-linear regression analyses were conducted using the SAS software program (PROC NLIN; version 9.3; SAS Institute Inc., Cary, NC, USA). Data were analyzed separately for each year and each cultivar by analysis of variance followed by a Tukey's test for means comparisons. Analysis of variance and mean comparison tests were conducted using the SAS software program (version 9.3, PROC ANOVA).

Results

Over the 3 years of the experiment, more mildew developed in the plots planted with the cultivar Chancellor, followed by the plots with the cultivar Vidal and then by those with the cultivar Seyval Blanc (Figs. [2](#page-4-0), [3](#page-4-0), and [4\)](#page-5-0). Regardless of the cultivar, mildew severity was highest during the 2010 season, followed by 2011 and then 2009 (Figs. [2,](#page-4-0) [3,](#page-4-0) and [4\)](#page-5-0). In general, the first mildew symptoms were observed during the first week of June and mildew severity increased until about 40 days before harvest, after which point downy mildew severity decreased until harvest.

For the cultivar Chancellor, regardless of the sampling year, no mildew was observed at 25 % bloom when the previous fall leaf mildew incidence had been below 5 % diseased leaves (Table [1\)](#page-6-0). In plots with a previous fall incidence of $>5\%$ to 10 %, PLAD_{bloom} was significantly different ($P < 0.001$) from that of plots with previous fall incidence of 0 % to 2.5 % in all years except 2009 (Table [1\)](#page-6-0). In the plots with a previous fall mildew incidence of $>10\%$ to 20 %, PLAD_{bloom} was significantly different ($P < 0.001$) from that of plots with lower fall mildew inci-dences (Table [1\)](#page-6-0). It was observed that $PLAD_{harvest}$,

Fig. 2 Temporal progress of grape downy mildew caused by Plasmopara viticola in plots planted in 2003 with the cultivar Chancellor. Percent leaf area diseased was monitored weekly in plots with different levels of fall mildew incidence. Symbols represent the mean values over 24 vines (three replications \times eight vines) and their standard error

AUDPC_{std}, and rate of disease progress (b) increased as previous fall mildew incidence increased (Table [1\)](#page-6-0). In plots with previous fall incidence $>10\%$ to 20 % mildewed leaves per vine, the time at which the cumulative proportion of leaf area diseased (PCPLAD) was one half of the maximum (x_0) was delayed by 20.2, 21.9, and 21.2 d in comparison with plots with previous fall incidence of 0 % to 2.5 % (Table [1\)](#page-6-0). Significant yield reductions ($P < 0.001$) were observed in the plots with a previous fall mildew incidence of $>10\%$ to 20 %, in the plots with a previous fall incidence of $>5\%$ to 10 % in 2010 and 2011, and in the

Fig. 3 Temporal progress of grape downy mildew caused by Plasmopara viticola in plots planted in 2003 with the cultivar Vidal. Percent leaf area diseased was monitored weekly in plots with different levels of fall mildew incidence. Symbols represent the mean values over 24 vines (three replications \times eight vines) and their standard error

plots with a previous fall incidence of >2.5 % to 5 % in 2011 (Table [1](#page-6-0)).

For the cultivar Vidal, regardless of the sampling year, no mildew was observed at 25 % bloom $(PLAN_{bloom})$ when leaf mildew incidence in the previous fall had been below 5 % diseased leaves (Table [1\)](#page-6-0). In plots with a previous fall incidence of $>5\%$ to 10 %, PLAD_{bloom} was significantly different ($P < 0.001$) from that observed in plots with previous fall incidence of 0 % to 2.5 % in all years except 2009 (Table [2](#page-7-0)). In the plots with a previous fall mildew incidence of >10 % to 20 %, PLAD_{bloom} was significantly different ($P < 0.001$) from that observed in plots with lower fall mildew

Fig. 4 Temporal progress of grape downy mildew caused by Plasmopara viticola in plots planted in 2003 with the cultivar Seyval Blanc. Percent leaf area diseased was monitored weekly in plots with different levels of fall mildew incidence. Symbols represent the mean values over 24 vines (three replications \times eight vines) and their standard error

incidences (Table [2\)](#page-7-0). It was observed that $PLAD_{harvest}$, AUDPC_{std}, and rate of disease progress (b) increased as fall mildew incidence increased (Table [2\)](#page-7-0). In plots with previous fall incidence >10 % to 20 % mildewed leaves per vine, the time at which the cumulative proportion of leaf area diseased (PCPLAD) was one half of the maximum (x_0) was delayed by 21.1, 22.7, and 21.8 d in comparison with plots previous fall incidence of 0 % to 2.5 % (Table [2\)](#page-7-0). Significant yield reductions were observed in the plots with a fall mildew incidence of more than 5% (Table [2\)](#page-7-0).

For the cultivar Seyval Blanc, regardless of the sampling year, no mildew was observed at 25 % bloom when the previous fall leaf mildew incidence had been below 10 % diseased leaves (Table [3\)](#page-8-0). For all 3 years, in plots with a previous fall incidence of $>10\%$ to 20 %, PLAD_{bloom} was significantly different ($P < 0.001$) from that of the plots with a previous fall incidence of 0 % to 2.5 % (Table [3](#page-8-0)). For all 3 years, PLADharvest, AUDPC_{std}, and rate of disease progress (b) increased as previous fall mildew incidence increased (Table [3](#page-8-0)). In plots with a previous fall incidence >10 % to 20 % mildewed leaves per vine, the time at which the cumulative proportion of leaf area diseased (PCPLAD) was one half of the maximum (x_0) was delayed by 23.9, 12.1, and 13.6 d in comparison with plots a previous fall incidence of 0 % to 2.5 % (Table [3](#page-8-0)). Significant yield reductions were observed only in the plots with a fall mildew incidence of >10 % to 20 % in 2010 (Table [3\)](#page-8-0).

Discussion

In grape production for wine making, the selection of cultivars is a critical decision. It will influence the type of wine that can be produced, yield, pest management, training systems, and, in northern areas, the winter protection practices that are used. In general, the management of diseases, including downy mildew, is concentrated during the period from bud break to nouaison and planned on a year-by-year basis. However, winter protection practices aiming to keep temperatures around the lower parts of the vines above −15 °C may favor the survival of P. viticola oospores, suggesting that management strategies should be planned on a multiyear basis. In other words, the efficacy of downy mildew management in a given year might have an influence on the risk of mildew in the next year. In this study, the influence of fall downy mildew expressed as the percent diseased leaves at harvest on disease progress during the next growing season was studied. Specifically, we looked at the temporal progress of downy mildew and mildew severity at bloom, the most critical vine growth stage, by investigating the leaf mildew severity at the beginning of bloom (25 % bloom), the time until the epidemic reached 50 % of its maximum, and the rate of mildew progress. For the highly susceptible cultivar Table 1 Variables used to describe downy mildew (Plasmopara viticola) in vineyard plots with different previous fall mildew incidences. The vineyard plots were planted with the grape cultivar Chancellor, and mildew severity was monitored during the 2009, 2010, and 2011 growing seasons

^a PLAD_{bloom} represents the percent leaf area diseased at 25 % bloom

^b PLAD_{harvest} represents the percent leaf area diseased at harvest

^c AUDPC_{std} represents the area under the disease progress curve standardized for the epidemic duration

 d_{x_0} represents the time at which the proportion of the maximum cumulative percent leaf area diseased is one half of the maximum

^e *b* represents the rate of disease progress

^f Yield expressed as the total weight in kilograms of marketable clusters per vine

^g For each year, values within a column with the same letter are not significantly different based on a Tukey's test at the 0.05 level of confidence

Chancellor, from 0.57 % to 10.47 % leaf area diseased was observed at the beginning of bloom in the vine plots with a fall incidence of more than 5 %, and significant yield reductions were observed in those plots. Similar effects of fall mildew incidence were observed for the cultivars Vidal and Seyval Blanc, indicating that regardless of cultivar susceptibility, the incidence of downy mildew in one year will have an influence on the risk of disease in the next year.

For several years, there was a consensus in the scientific literature on grape downy mildew that disease is initiated by only a few primary infections occurring within a short period in the spring and that disease progress and consequent yield reductions are driven mostly by secondary infections (Gessler et al. [2011\)](#page-9-0). However, recent work by Gobbin et al. ([2003,](#page-9-0) [2005\)](#page-9-0) highlighted the importance of oospore infection in downy mildew epidemics. Without diminishing the importance of secondary infections, their work clearly showed the potential of oospores to germinate over

relatively long periods and hence the significance of primary inoculum in grape downy mildew epidemics (Gobbin et al. [2003](#page-9-0), [2005](#page-9-0)). Nevertheless, several factors influence the severity of downy mildew epidemics and potential yield losses. The first factor is the combined oospore-induced primary infections period and polycyclic (sporangiainduced secondary infections) nature of the disease, as well as the possible overlap of both inoculum types. The second factor is the weather conditions, which influence each stage of pathogen development (Rossi et al. [2009\)](#page-10-0). The third factor is the susceptibility of the grape variety and temporal changes in organ susceptibility during the growing season. In practice, therefore, the risk of grape downy mildew is modulated by the synchronicity of a sufficient amount of inoculum (primary and secondary), favorable weather conditions, and vine-organ susceptibility. The results of this study suggest that when high numbers of leaves are infected in the fall $(5\frac{9}{0})$, a higher amount of primary inoculum (oospores) will be present in the

Year	Fall mildew incidence	$PLAD_{bloom}^a$	$PLADharvest$ _b	$AUDPCstd$ ^c	$x_0^{\ d}$	B^e	Yield ^t
2009 ^g	$0.0 - 2.5 \%$	0.00 _b	3.96c	0.98d	246.19a	4.00c	1.67a
2009	$>2.5-5.0\%$	0.00 _b	7.99b	3.12c	240.64b	7.11bc	1.79a
2009	$>5.0 - 10.0\%$	0.34 _b	8.65b	6.01 _b	236.06c	9.11b	1.56ab
2009	$>10.0 - 20.0$ %	2.72a	13.72a	13.09a	225.10d	14.43a	1.29b
2010	$0.0 - 2.5 \%$	0.00 _b	2.59d	1.27d	240.10a	7.08c	1.53a
2010	$>2.5-5.0\%$	0.00 _b	6.58c	4.64c	225.90b	10.39 _b	1.38a
2010	$>5.0 - 10.0\%$	6.63a	9.51 _b	11.04b	217.30c	12.56a	0.97 _b
2010	$>10.0 - 20.0$ %	6.64a	14.58a	25.12a	217.40c	13.59a	1.02 _b
2011	$0.0 - 2.5 \%$	0.00c	1.84d	0.71d	232.90a	4.61c	1.72a
2011	$>2.5-5.0\%$	0.00c	5.14c	4.18c	221.80b	7.73 _b	1.97a
2011	$>5.0 - 10.0\%$	3.65 _b	7.99b	8.65b	213.50c	11.66a	0.92 _b
2011	$>10.0 - 20.0$ %	6.32a	10.71a	18.66a	211.10c	11.88a	0.86 _b

Table 2 Variables used to describe downy mildew (Plasmopara viticola) in vineyard plots with different previous fall mildew incidences. The vineyard plots were planted with the grape cultivar

Vidal, and mildew severity was monitored during the 2009, 2010, and 2011 growing seasons

^a PLAD_{bloom} represents the percent leaf area diseased at 25 % bloom

^b PLAD_{harvest} represents the percent leaf area diseased at harvest

^c AUDPC_{std} represents the area under the disease progress curve standardized for the epidemic duration

 d_{x_0} represents the time at which the proportion of the maximum cumulative percent leaf area diseased is one half of the maximum

^e *b* represents the rate of disease progress

^f Yield expressed as thwe total weight in kilograms of marketable clusters per vine

^g For each year, values within a column with the same letter are not significantly different based on a Tukey's test at the 0.05 level of confidence

following spring, favoring the synchronicity between the presence of inoculum and the susceptibility of inflorescences. Downy mildew epidemics were advanced on average by 22, 22, and 16 d for the highly susceptible cultivar Chancellor, the moderately susceptible cultivar Vidal, and the slightly susceptible cultivar Seyval Blanc, respectively. For polycyclic diseases such as grape downy mildew this period of time is critical as it allows for more infection cycles and consequently faster secondary inoculum build-up. In addition, in the context of northern viticulture, where in the spring the vines are cut back to about 30 to 40 cm from the ground soon after the winter protection is removed, the earlier appearance of leaf symptoms and the reduced number of healthy inflorescences per vine might be explained by oospore infection of leaves and inflorescences that are near the ground and hence are exposed to zoospore infections. Nevertheless, considering that downy mildew develops first on leaves, which serve as inoculum reservoirs for inflorescence and cluster infections, and that zoospores are produced continuously, early infections are synonymous with higher yield losses (Savary et al. [2009\)](#page-10-0).

For several polycyclic diseases with both primary and secondary inoculum, it is often assumed that primary inoculum is always present in sufficient amounts to initiate epidemics. This was the case for apple scab caused by Venturia inaequalis; for that disease, it was shown that the amount of disease in the fall has a significant influence on scab development in the next season and that epidemics are delayed when inoculum potential is low (MacHardy et al. [1993;](#page-9-0) Reardon et al. [2005](#page-9-0)). Consequently, treatments aimed at reducing overwintering inoculum mean that less fungicide is needed to control apple scab during the next growing season (Carisse and Rolland [2004;](#page-9-0) Sutton et al. [2000\)](#page-10-0). The amount of initial inoculum could be predicted based on fall disease incidence and winter weather conditions (Reardon et al. [2005\)](#page-9-0) or monitored using spore samplers (Charest et al. [2002](#page-9-0)). Another approach is to assume that there Table 3 Variables used to describe downy mildew (Plasmopara viticola) in vineyard plots with different previous fall mildew incidences. The vineyard plots were planted with the grape cultivar Seyval Blanc, and mildew severity was monitored during the 2009, 2010, and 2011 growing seasons^y

^a PLAD_{bloom} represents the percent leaf area diseased at 25 % bloom

^b PLAD_{harvest} represents the percent leaf area diseased at harvest

^c AUDPC_{std} represents the area under the disease progress curve standardized for the epidemic duration

 d_{x_0} represents the time at which the proportion of the maximum cumulative percent leaf area diseased is one half of the maximum

^e *b* represents the rate of disease progress

^f Yield expressed as thwe total weight in kilograms of marketable clusters per vine

^g For each year, values within a column with the same letter are not significantly different based on a Tukey's test at the 0.05 level of confidence

is a relationship between disease incidence and severity in the fall and the amount of primary inoculum in the following spring (MacHardy et al. [1993](#page-9-0); Reardon et al. [2005](#page-9-0)). When such a relationship exists, assessing the disease level in the fall is easier than measuring primary inoculum in the following spring

This study was conducted in plots where the vines were protected during the winter months, and hence it is probable that most oospores survived the winter. The results of our study clearly show that fall mildew incidence is related to mildew progress and yield reduction during the following growing season. However, it is likely that in vineyards without winter protection, there is a similar relationship between fall disease incidence and primary inoculum in the following spring, although the environment probably has a greater influence on oospore survival when the vines are not protected. Consequently, the relationship between fall disease incidence or severity and downy mildew behavior in the following spring must be established before the results from this study can be transposed to other regions and other vineproduction systems. Nevertheless, information on fall downy mildew incidence is of great value for decisions about downy mildew management. In practice, if information on fall mildew incidence is to be included in management decisions during the following season, an appropriate sampling plan must be developed so that the time and reliability of sampling are optimal (Carisse et al. [2009](#page-9-0)).

Management decisions about grape downy mildew, as with most important crop diseases, should be based on long-term strategic decisions about matters such as cultivars, vineyard establishment conditions (row orientation and spacing), and training systems. Short-term or tactical decisions about grape downy mildew management must be taken based on in-field information such as weather-based forecasts of the time of primary lesion emergence (Caffi et al. [2011\)](#page-9-0) and the potential primary inoculum dose.

Acknowledgments This work was financially supported by Agriculture and Agri-Food Canada. The author would like to thank Annie Lefebvre for providing technical assistance and guidance in conducting the experiments.

References

- Blouin, J. (2007). Les parasites de la vigne : stratégies de protection raisonnée. Éditions Dunod, 196 pp. ISBN: 978–2–1004– 9995–3.
- Caffi, T., Rossi, V., Bugiani, R., Spanna, F., Flamini, L., Cossu, A., & Nigro, C. (2009). Evaluation of a model predicting primary infections of Plasmopara viticola in different grapevinegrowing areas of Italy. Journal of Plant Pathology, 91, 535–548.
- Caffi, T., Rossi, V., & Carisse, O. (2011). Evaluation of a dynamic model for primary infections caused by Plasmopara viticola on grapevine in Quebec. Plant Health Progress. doi[:10.1094/](http://dx.doi.org/10.1094/PHP-2011-0126-01-RS) [PHP-2011-0126-01-RS.](http://dx.doi.org/10.1094/PHP-2011-0126-01-RS)
- Carisse, O., Meloche, C., Boivin, G., & Jobin, T. (2009). Action thresholds for summer fungicide sprays and sequential classification of apple scab incidence. Plant Disease, 93, 490– 498.
- Carisse, O., & Rolland, D. (2004). Effect of timing of application of the biological control agent Microsphaeropsis ochracea on the production and ejection pattern of ascospores by Venturia inaequalis. Phytopathology, 94, 1305–1314.
- Charest, J., Dewdney, M., Paulitz, T., Philion, V., & Carisse, O. (2002). Spatial distribution of Venturia inaequalis airborne ascospores in orchards. Phytopathology, 92, 769–779.
- Davidou, L., & Crachereau, J.-C. (2011). Mise en évidence de l'impact qualitatif de la présence de mildiou Plasmopara viticola en faciès rot brun sur les vins rouges de Bordeaux et détermination de seuils de tolérance. Revue Oenologues, 139, 16–19.
- Dubos, B. (2002). Maladies cryptogamiques de la vigne : champignons parasites des organes herbacés et du bois de la vigne. 2nd ed. Éditions Féret, Bordeaux, France. pp. 17–32. ISBN: 978–2–9024–1677–6.
- Galet, P. (1977). In Les maladies et les parasites de la vigne (vol. 1: Les maladies dues à des végétaux, p. 871). Montpellier, France: Imprimerie du Paysan du Midi.
- Gessler, C., Pertot, I., & Perazzolli, M. (2011). Plasmopara viticola: a review of knowledge on downy mildew of grapevine and effective disease management. Phytopathologia Mediterranea, 50, 3–44.
- Gobbin, D., Jermini, M., Loskill, B., Pertot, I., Raynal, M., & Gessler, C. (2005). Importance of secondary inoculum of Plasmopara viticola to epidemics of grapevine downy mildew. Plant Pathology, 54, 522–534.
- Gobbin, D., Pertot, I., & Gessler, C. (2003). Identification of microsatellite markers for Plasmopara viticola and establishment of high throughput method for SSR analysis. European Journal of Plant Pathology, 109, 153–164.
- Hill, G. K. (2000). Simulation of P. viticola oospore-maturation with the model SIMPO. *IOBC/WPRS Bulletin*, 23(4), 7–8.
- Springer
- Jermini, M., Blaise, P., & Gessler, C. (2010). Quantitative effect of leaf damage caused by downy mildew (Plasmopara viticola) on growth and yield quality of grapevine 'merlot' (Vitis vinifera). Vitis, 49, 77–85.
- Jolivet, Y., & Dubois, J.-M. M. (2000). Évaluation de l'efficacité du buttage de la vigne comme méthode de protection contre le froid hivernal au Québec. Journal International des Sciences de la Vigne et du Vin, 34, 83–92.
- Kennelly, M. M., Gadoury, D. M., Wilcox, W. F., Magarey, P. A., & Seem, R. C. (2005). Seasonal development of ontogenic resistance to downy mildew in grape berries and rachises. Phytopathology, 95, 1445–1452.
- Kennelly, M. M., Gadoury, D. M., Wilcox, W. F., Magarey, P. A., & Seem, R. C. (2007). Primary infection, lesion productivity, and survival of sporangia in the grapevine downy mildew pathogen Plasmopara viticola. Phytopathology, 97, 512–522.
- Kiefer, B., Riemann, M., Büche, C., Kassemeyer, H.-H., & Nick, P. (2002). The host guides morphogenesis and stomatal targeting in the grapevine pathogen Plasmopara viticola. Planta, 215, 387–393.
- Lalancette, N., Ellis, M. A., & Madden, L. V. (1987). Estimating infection efficiency of Plasmopara viticola on grape. Plant Disease, 71, 981–983.
- MacHardy, W. E., Gadoury, D. M., & Rosenberger, D. A. (1993). Delaying the onset of fungicide programs for the control of apple scab in orchards with low potential ascospore dose of Venturia inaequalis. Plant Disease, 77, 372–375.
- Ontario Ministry of Agriculture, Food & Rural Affairs. (2008). Fruit Production Recommendations 2008–2009. Publication 360. Ontario Ministry of Agriculture, Food and Rural Affairs, Toronto, ON, Canada.
- Orlandini, S., Massetti, L., & Dalla Marta, A. (2008). An agrometeorological approach for the stimulation of Plasmopara viticola. Computers and Electronics in Agriculture, 64, 149–161.
- Park, E. W., Seem, R. C., Gadoury, D. M., & Pearson, R. C. (1997). DMCAST: a prediction model for grape downy mildew development. Viticulture Enology Science, 52, 182–189.
- Reardon, J. E., Berkett, L. P., Garcia, M. E., & Gotlieb, A. (2005). Field evaluation of a new sequential sampling technique for determining apple scab "risk". Plant Disease, 89, 228–236.
- Riemann, M., Büche, C., Kassemeyer, H.-H., & Nick, P. (2002). Cytoskeletal responses during early development of the downy mildew of grapevine (Plasmopara viticola). Protoplasma, 219, 13–22.
- Rosa, M., Gozzini, B., Orlandini, S., & Seghi, L. (1995). A computer program to improve the control of grapevine downy mildew. Computers and Electronics in Agriculture, 12, 311–322.
- Rossi, V., & Caffi, T. (2012). The role of rain in dispersal of the primary inoculum of Plasmopara viticola. Phytopathology, 102, 158–165.
- Rossi, V., Caffi, T., Bugiani, R., Spanna, F., & Della Valle, D. (2008a). Estimating the germination dynamics of Plasmopara viticola oospores using hydro-thermal time. Plant Patholology, 57, 216–226.
- Rossi, V., Caffi, T., Giosuè, S., & Bugiani, R. (2008b). A mechanist model simulating primary infections of

downy mildew in grapevine. Ecological Modelling, 212, 480–491.

- Rossi, V., Giosuè, S., & Caffi, T. (2009). Modelling the dynamics of infections caused by sexual and asexual spores during Plasmopara viticola epidemics. Journal of Plant Pathology, 91, 615–627.
- Rouzet, J., & Jacquin, D. (2003). Development of overwintering oospores of Plasmopara viticola and severity of primary foci in relation to climate. EPPO Bulletin, 33, 437–442.
- Savary, S., Delbac, L., Rochas, A., Taisant, G., & Willocquet, L. (2009). Analysis of nonlinear relationships in dual epidemics, and its application to the management of grapevine downy and powdery mildews. Phytopathology, 99, 930–942.
- Vercesi, A., Tornaghi, R., Sant, S., Burruano, S., & Faoro, F. (1999). A cytological and ultrastructural study on the maturation and germination of oospores of Plasmopara viticola from overwintering vine leaves. Mycological Research, 103, 193–202.
- Viret, O., & Siegfried, W. (1996). Fiche technique sur les maladies de la vigne: mildiou. Revue Suisse de Viticulture Arboriculture Horticulture, 28, 373–374.