# ELABORATION AND VALIDATION OF A DYNAMIC MODEL FOR PRIMARY INFECTIONS OF *PLASMOPARA VITICOLA* IN NORTH ITALY

## ELABORAZIONE E VALIDAZIONE DI UN MODELLO DINAMICO PER LE INFEZIONI PRIMARIE DI *PLASMOPARA VITICOLA* IN NORD ITALIA

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## Abstract

A dynamic model simulating the life cycle of *Plasmopara viticola*, from overwintering oospores to the appearance of primary symptoms on grape leaves, was elaborated in order to obtain accurate and robust information about the risk for downy mildew infections during the primary inoculum season. The model was elaborated according to the systems analysis, and takes into account the following stages of the infection cycle: oospore maturation and germination, survival of zoosporangia and zoospore ejection, survival and dispersal of zoospores, infection and incubation. The model allows to evaluate hourly the progress of the infection process, and to estimate the period of disease symptom onset. The model was validated against data not used for model elaboration. Hourly meteorological data were collected under different epidemiological conditions (several locations and years) in northern Italy (Piedmont, Oltrepò Pavese, and Emilia-Romagna), and simulations were compared with actual disease appearance observed in vineyards. The model proved to be accurate and robust.

***Keywords:*** Downy mildew, grapevine, oospores, primary infections, dynamic model

## *Riassunto*

*È stato elaborato un modello epidemiologico che simula la dinamica delle infezioni primarie di* Plasmopara viticola*, sulla base delle condizioni meteorologiche del periodo invernale e primaverile. Il modello simula in itinere, con cadenza oraria, le fasi di latenza e germinazione delle oospore, sopravvivenza degli sporangi, liberazione delle zoospore, loro dispersione, infezione ed incubazione. Il modello è stato validato con dati meteorologici non impiegati nella sua elaborazione; questi ultimi sono stati raccolti in differenti condizioni epidemiologiche (diverse località e anni) del Piemonte, dell'Oltrepò Pavese e dell'Emilia-Romagna. Le simulazioni sono state confrontate con la reale comparsa dei sintomi in campo. Il modello ha fornito simulazioni accurate e robuste.*

***Parole chiave:*** *Peronospora, vite, oospore, infezioni primarie, modello dinamico*

## Introduction

Grapevine downy mildew, caused by the fungus *Plasmopara viticola* (Berk. *et* Curt.) Berl. *et* De Toni, occurs throughout the world. It attacks mainly the varieties of *Vitis vinifera*, which constitute the most part of vineyards under cultivation, and development of its epidemics is strongly influenced by climate (Lafon and Bulit, 1981). Downy mildew originates from North America and it has been introduced in Europe through American rootstocks at the end of 19$^{th}$ century; in 1880, the fungus had already invaded all France vineyards and it spread throughout Europe, some areas of Asia and Africa. However, twenty years passed till the occurrence of the first really disastrous epidemic, in 1900, when about 70% of the expected yield was completely destroyed (Müller and Sleumer, 1934; Sarejanni, 1951). Since then, downy mildew constitutes the most damaging disease of grapevine in the European humid areas.

The biological cycle of *P. viticola* includes an asexual stage, which is responsible for the secondary infection cycles occurring during the host-growing season, and a sexual stage, that ensures survival of the pathogen over winter and produces the inoculum for primary infections in spring. Epidemiological parameters involved in the development of the secondary infections are well known (Lalancette, 1987; Lalancette *et al.*, 1988); on the contrary, there is a lack of knowledge on the condition fa-

voring oospore formation, maturation and germination. This is a key stage for the disease, because zoospores, released from zoosporangia originated from oospores, are responsible for primary infections. Recently, the role of oospores in the epidemiology of *P. viticola* was reconsidered (Gessler *et al.*, 2003), because they constitute an important source of inoculum for a long period during the season, frequently overlapping secondary cycles and sometimes even prevailing over the secondary inoculum (Park *et al.*, 1997).

Fungicides are the most important control measure on susceptible varieties grown in areas with high disease pressure. Traditionally, fungicides are applied at fixed intervals (7-14 days) in order to maintain the host surface constantly covered by an effective dose of chemicals. Usually, 8 to 12 treatments are required per growing season (Orlandini *et al.*, 1993). Timing of these applications is crucial for their efficacy, because anticipated or delayed sprays have little or no effect on disease epidemics (Costa and Rosa, 1998).

In order to better determine optimal time for fungicide applications, epidemiological models were introduced to estimate disease risk and produce warnings for fungicide applications. Several models were elaborated to describe the infection process of downy mildew, with particular emphasis for primary infections. The EPI model (Stryzik, 1983) is aimed at simulating the behavior of *P. viticola* through its energetic state and the infectious potential (Vercesi *et al.*, 1999). The POM model, elaborated in France (Tran Manh Sung *et al.*, 1990), is a climate-based empirical model that allows to determine the Date of Optimum Maturation for oospores for the Bordeaux area. The SIMPO model (Hill, 2000) indicates the number of days required for oospores germination and, therefore, the potential risk of primary infections (Gobbin *et al.*, 2003). The DMCAST model uses the same parameters of the POM model, and predicts the date of primary infection when almost 3% of oospores are ready to germinate (Park *et al.*, 1997).

None of these models is sufficiently accurate and robust to be used in disease warning under Italian conditions (Vercesi *et al.*, 1999; Vercesi and Liberati, 2001). Therefore, the so called "3-10" empiric rule is widely used in warning systems operating throughout Italy (Rossi *et al.*, 2000), even if it often produces unjustified alarms (Brunelli and Cortesi, 1990; Vercesi, 1995; Serra *et al.*, 1998). This rule is based on the satisfaction of the following conditions: i) air temperature, in 24 hours, must be equal to or greater than 10°C; ii) shoot length must be at least 10 cm; iii) at least 10 mm of rain must fall within 24-48 hours (Goidanich *et al.*, 1957).

A dynamic model simulating the sexual stage of *P. viticola* was then elaborated using the systems analysis, a tool that allow the modeling of pathosystems with a mechanicistic approach (Rossi *et al.*, 1997) instead of the empirical one used in the existing models for downy mildew primary infections.

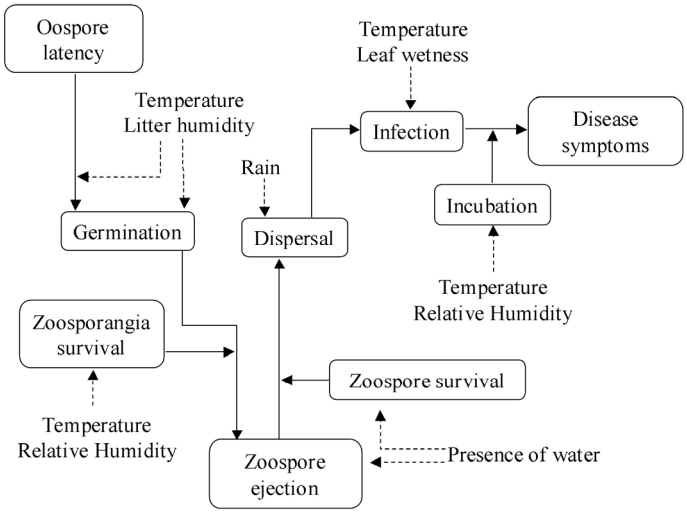


**Fig. 1** – Diagram showing the conceptual model simulating primary infections caused by *P. viticola* on grape

***Fig. 1** – Diagramma del modello di simulazione delle infezioni primarie causate da* P. viticola

## Material and Methods

### Model description

The model was elaborated according to the principles of systems analysis (Leffelaar, 1993). The conceptual model is shown in Fig. 1. It takes into account the following stages of the infection cycle of *P. viticola*, which are considered as state variables: oospore maturation and germination, survival of sporangia and zoospore ejection, zoospore survival and dispersal, infection and incubation. Changes from a state variable to another depend on environmental conditions during winter and spring, in particular on air temperature, relative humidity, leaf wetness and rainfall. In the model, mathematical equations relate these meteorological (driving) variables to the rates at which each state variable changes. A detailed description of the model will be published in a separated paper.

Oospores are the overwintering stage of the fungus; they have a latent period that does not allow them to germinate when there is not a susceptible host tissue. In the model, overcoming of latency is calculated by a maturation rate which depends on environmental conditions (Oospore Maturation Index, IMO). IMO increases hourly from January 1$^{st}$, at a variable rate depending on air temperature and humidity of the leaf litter containing oospores; rate of progress is equal to zero when the leaf litter humidity is too low and there is no rain or wetness. Humidity of the leaf litter is calculated as a function of the vapour pressure deficit. After a fixed threshold, the model assumes that subsequent cohorts of oospores

overcome the latency within a time interval defined by a minimum and maximum value of IMO.
The model begins the germination process of a cohort of oospores every time that rainfall moistens the leaf litter (rainfall ≥ 0.2 mm/hour). The rate of oospore germination (ΔGER ) depends on temperature (Laviola *et al.*, 1986), when humidity of the leaf litter is not a limiting factor. The model considers that the oospore cohort has germinated and produced zoosporangia when summation of ΔGER is equal or greater than 1. At this stage, zoosporangia are present on the leaf litter.
In the absence of water, sporangia can survive for 6 hours to 6 days, according to the environmental conditions (Blaeser and Weltzien, 1979). Maximum duration of survival (SURmax, in days) is calculated as a function of temperature and relative humidity. Then the model calculates the hourly progress of survival as ΔSUR=1/(SURmax·24): when summation of the hourly values of ΔSUR is lower than 1, there are viable sporangia on the leaf litter.
The model simulates zoospore ejection from zoosporangia based on wetness and temperature (Ravaz, 1914; Galet, 1977); a specific equation calculates LWger as the minimum number of hours required for sporangia to germinate. At this stage, zoospores are swimming in the film of water wetting the leaf litter; they survive in such a condition until the water persists, but they quickly die when there is no longer water. The model assumes that, during the period of zoospore survival, rainfall (at least of 0.2 mm/hour) produces the splash-dispersal of zoospores to leaves.
The possibility that zoospores immigrated on a susceptible leaf blade cause infection depends on a combination of favorable conditions of temperature and wetness duration (Blaeser, 1978). Following a successful infection, the model calculates the length of the incubation period as a function of temperature and relative humidity (Goidanich *et al.*, 1957). The model uses two regression equations relating temperature to the length of incubation, at two extreme levels of relative humidity. Therefore the model produces a period when disease symptoms should occur.
Model outputs can be produced both as a data sheet with a hourly time step, or as a graph (Fig. 2).

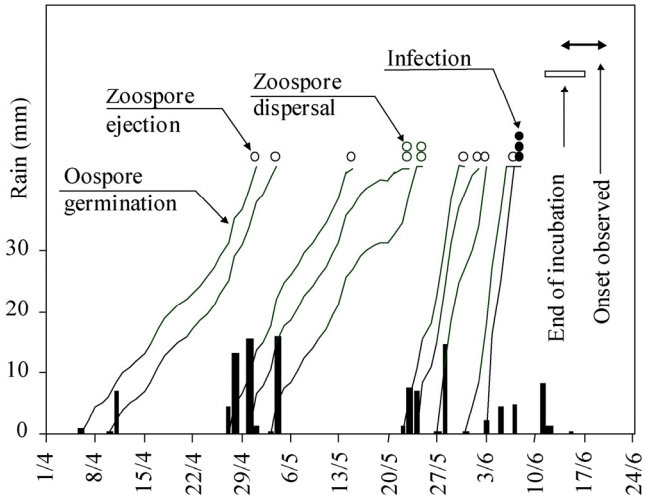


**Fig. 2** – Example of the output produced by the model simulating primary infections caused by *P. viticola* on grape: bars represent the daily amount of rainfall; lines show the progress of germination in different cohorts of oospores; dots show the occurrence of the different stages of the infection cycle, from zoospore ejection to leaf infection (dots are black when the infection cycle is successfully completed); box shows the period of the expected appearance of downy mildew symptoms, while the arrow shows the actual disease onset in vineyard

***Fig. 2** – Esempio dell'output fornito dal modello di simulazione delle infezioni primarie causate da* P. viticola*; le barre indicano la pioggia giornaliera; le linee mostrano l' avanzamento della germinazione delle diverse coorti di oospore mature; i cerchi indicano il verificarsi dei differenti passaggi del ciclo di infezione, dal rilascio delle zoospore da parte del macrozoosporangio fino all'infezione dei tessuti dell'ospite (i cerchi sono neri quando il ciclo è completo); il rettangolo mostra il periodo in cui dovrebbero comparire i sintomi di peronospora, mentre la doppia freccia mostra il periodo di reale comparsa osservata in vigneto*

**Model validation**
Validations were performed in commercial vineyards, in big plots not sprayed with fungicides against downy mildew until the time of first disease onset. Vineyards were representative of the crop in the vine-growing area considered, for soils, varieties, training systems and cropping regimes. A regular fungicides scheduling in the previous season ensured a representative dose of overwintering inoculum. Validations were performed between 1995 and 2004 at several locations in the Emilia-Romagna region, between 1999 and 2004 at 5 locations in Piedmont, and between 1998 and 2002 at one site in Oltrepò Pavese (Lombardy). Starting from bud burst, vineyards were carefully inspected at least one time per week, to point out the time of appearance of first disease symptoms, as "oil spots" on leaves.
To run the model, hourly meteorological data of air temperature, relative humidity, rainfall, and leaf wetness were collected. In Piedmont and Oltrepò Pavese, data were measured by automatic and mechanic weather stations, respectively, installed within the vineyards. In Emilia-Romagna, meteorological data were supplied by the agrometeorological regional network; until the year 2000 the service supplied, for each vineyard, meteorological data from the nearest automatic station, while from the year 2001 it supplied data interpolated on a grid of 5x5 km.
The model was used to simulate, for each vineyard, the infection process in each cohort of oospores between the end of latency and the time of first disease onset in the vineyard. Total simulations were firstly distinguished in

aborted and successful. A simulation was considered aborted when the infection process stopped in any stage before infection, while it was considered successful when all the stages progressed until infection establishment. Both aborted and successful simulations were then distinguished in: i) accurate, when the model produced a successful simulated infection that actually produced symptom appearance, or when an aborted simulated infection did not correspond to an actual symptom onset; ii) overestimated, when the model produced a successful simulated infection but the disease did not appear; iii) underestimated, when the model did not simulate an infection that actually occurred. A possible criticism of the above mentioned classification is that there is no proof that an aborted simulation process actually occurred in the vineyard; nevertheless, under a practical point of view, the model produces an accurate information in such a case, because it signals that there is not risk for infection to occur.

## Results And Discussion

Model outputs were validated in 62 vineyards, in different vine-growing areas of northern Italy (Tab. 1). In Emilia-Romagna, the model was validated under 38 different epidemiological conditions. 365 simulations were performed in aggregate: 339 of them were accurate, while 26 were overestimated. In Oltrepò Pavese, the model was tested in the same vineyard for a 5-year period, and it provided 26 simulations: 13 of them aborted during the infection process, 12 simulated correctly the disease onset, and in only one case disease appearance was overestimated. In Piedmont, the model was validated in 19 different situations: it provided 153 simulations, with 109 simulations aborted. In 38 cases, the model simulated correctly the onset of primary downy mildew infections, with 6 unjustified alarms. The model never failed to signal an actual infection.

In aggregate, the model produced 544 simulations: the $\chi^2$ test showed a significant association between model simulations and actual observations (Tab. 2). The model was very accurate in simulating successful infections, because all the observed disease appearances in the vineyards were correctly simulated by the model; it occurred 97 times (18% of simulations) (Tab. 2).

Disease symptoms were never observed when the model did not signal a successful infection; it occurred in 414 cases (76%) (Tab. 2). In all these cases, the model interrupted its simulations because environmental conditions did not permit the progress of the infection cycle. In particular, 46 simulations were interrupted before zoospore ejection, because of the lack of wetness during the survival time of zoosporangia produced on the leaf litter, so that they died before ejecting zoospores. In 327 cases, the infection cycle was interrupted because no rain fell when viable zoospores were present in the film of water wetting the leaf litter, so that zoospores died before reaching susceptible vine leaves. Finally, 41 simulations aborted because zoospores did not encounter favorable

**Tab. 1** – Main results obtained by the model simulating the primary infections caused by *P. viticola* on grape. Simulations were made for 62 vineyards in aggregate, over three regions, in many years, and compared with actual disease appearance. Total simulations are distinguished in accurate and overestimated; accurate simulations were distinguished in aborted (because either no zoospore ejection, or no zoospore dispersal, or no leaf infection occurred) and successful infections

***Tab. 1*** *– Principali risultati forniti dal modello nella simulazione delle infezioni primarie causate da* P. viticola*. Le simulazioni sono state condotte complessivamente in 62 vigneti, di tre differenti regioni e in diversi anni, e confrontate con la reale comparsa dei sintomi di malattia. Il totale delle simulazioni è suddiviso in accurate e sovrastimate; le simulazioni accurate sono divise in interrotte (perché non si sono verificate il rilascio o la diffusione delle zoospore, oppure l'infezione) e in efficaci*

| Region /Year | N° of vineyards | Total simulations | Accurate aborted infections | No zoospore ejection | No zoospore dispersal | No leaf infection | Accurate successful infections | Overestimated infections |
|---|---|---|---|---|---|---|---|---|
| Emilia-Romagna | | | | | | | | |
| 1995 | 3 | 18 | 11 | -- | 11 | -- | 6 | 1 |
| 1996 | 4 | 19 | 16 | -- | 13 | 3 | 3 | 0 |
| 1997 | 4 | 70 | 61 | -- | 59 | 2 | 5 | 4 |
| 1998 | 4 | 40 | 32 | -- | 31 | 1 | 4 | 4 |
| 1999 | 2 | 16 | 13 | -- | 13 | -- | 2 | 1 |
| 2000 | 3 | 24 | 17 | -- | 17 | -- | 4 | 3 |
| 2001 | 5 | 42 | 33 | 1 | 24 | 8 | 8 | 1 |
| 2002 | 5 | 34 | 25 | -- | 22 | 3 | 7 | 2 |
| 2003 | 3 | 29 | 25 | 8 | 17 | -- | 4 | 0 |
| 2004 | 5 | 73 | 59 | 9 | 39 | 11 | 4 | 10 |
| Totale | 38 | 365 | 292 | 18 | 246 | 28 | 47 | 26 |
| Oltrepò Pavese | | | | | | | | |
| 1998 | 1 | 6 | 5 | -- | 5 | -- | 1 | - |
| 1999 | 1 | 5 | 3 | -- | 3 | -- | 1 | 1 |
| 2000 | 1 | 3 | 1 | -- | 1 | -- | 2 | - |
| 2001 | 1 | 6 | 2 | -- | 2 | -- | 4 | - |
| 2002 | 1 | 6 | 2 | -- | 2 | -- | 4 | - |
| Totale | 5 | 26 | 13 | -- | 13 | -- | 12 | 1 |
| Piedmont | | | | | | | | |
| 1999 | 1 | 5 | 4 | -- | 3 | 1 | 1 | - |
| 2000 | 1 | 4 | 2 | -- | 2 | -- | 1 | 1 |
| 2001 | 1 | 6 | 3 | -- | 1 | 2 | 3 | - |
| 2002 | 5 | 58 | 38 | 2 | 33 | 3 | 20 | - |
| 2003 | 6 | 41 | 35 | 21 | 10 | 4 | 2 | 4 |
| 2004 | 5 | 39 | 27 | 5 | 19 | 3 | 11 | 1 |
| Totale | 19 | 153 | 109 | 28 | 68 | 13 | 38 | 6 |

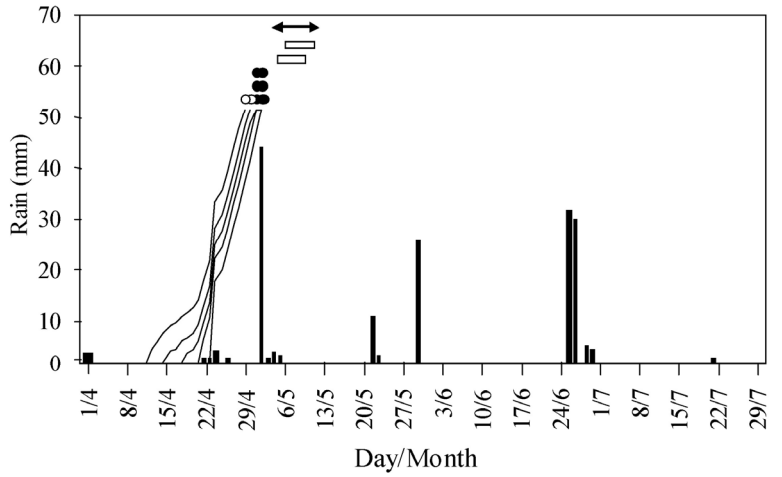


**Fig. 3** – Model simulations for Castelfranco Emilia (Modena), in 1996. The overcoming of oospore latency was simulated on April 10; the model provided two simulations aborted after zoospores ejection, while the simulations started on April 17, 21, and 23 completed the infection cycle, with expected onset of disease symptoms between May 5 and 9. Actual downy mildew onset was registered between May 5 and 11

***Fig. 3*** *– Simulazioni fornite dal modello a Castelfranco Emilia (Modena) nel 1996. Il superamento della latenza delle oospore è stato simulato il 10 aprile; il modello ha interrotto due simulazioni dopo il rilascio delle zoospore, mentre le simulazioni partite il 17, 21 e 23 aprile hanno completato il ciclo di infezione, prevedendo la comparsa dei sintomi tra il 5 e il 9 maggio. La reale comparsa dei sintomi in campo è stata registrata tra il 5 e l'11 maggio*

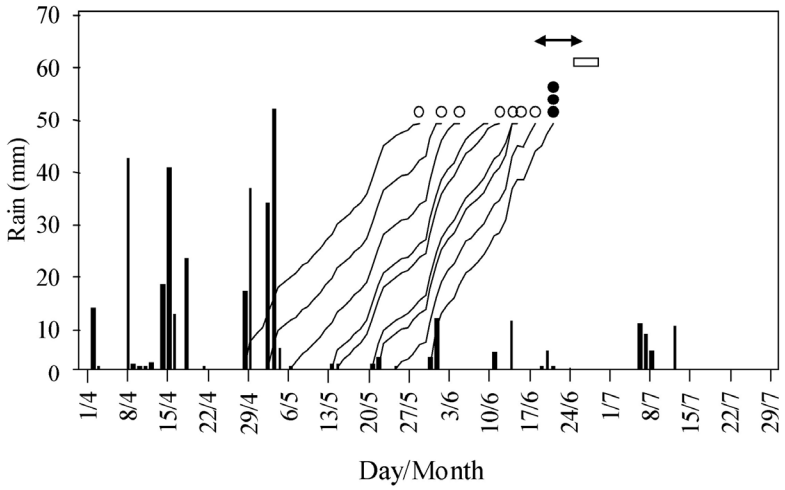


**Fig. 4** – Model simulations for Coazzolo (Asti), in 2004. The overcoming of oospores latency was simulated on April 29; the model produced eight simulations, seven of them aborted before zoospore dispersal and one aborted before zoospore ejection. Rainfall occurred on May 31 triggered a germination process that resulted in a successful infection on June 21. The appearance of symptoms was expected between June 25 and 28; actual disease onset was registered between June 18 and 25

***Fig. 4*** *– Simulazioni fornite dal modello a Coazzolo (Asti) nel 2004. Il superamento della fase di latenza è stato stimato al 29 aprile; il modello ha fornito otto simulazioni, delle quali settte interrotte prima della diffusione delle zoospore ed una interrotta prima del rilascio delle stesse da parte del macrozoosporangio. La pioggia del 31 maggio ha avviato un processo germinativo che si è concluso con l'avvenuta infezione dell'ospite il 21 giugno. La comparsa dei sintomi è stata stimata tra il 25 e il 28 giugno; la reale comparsa è stata registrata in campo tra il 18 e il 25 giugno*

conditions of temperature and wetness duration on the leaf surface, so that they did not establish infection.

Considering both successful and interrupted processes, accurate simulations were 511 out of 544 (94%) (Tab. 2). The model was accurate for both early and late infections; furthermore, it correctly simulated the absence of successful infections when downy mildew did not appear for the entire season.

An early infection occurred, for instance, at Castelfranco Emilia (Modena), in 1996 (Fig. 3). Oospore maturity was estimated on April 10. First and second cohorts of oospores did not complete their infection cycle because zoospores died before their dispersal. Simulations initiated by rainfall occurred on April 17, 21 and 23 resulted in complete infection cycles, with expected appearance of disease symptoms between May 5 and 9. First oil spots on leaves were found between May 5 and 11.

A late infection occurred at Coazzolo (Asti), in 2004 (Fig. 4). The model simulated oospore maturity on April 29. Simulations for the first eight cohorts of oospores were interrupted because environmental conditions were

**Tab. 2** – Comparison between the occurrence of primary infections caused by of *P. viticola* as observed in the vineyards of Tab. 1, and simulated by the model ($\chi^2$ = 373.6, using the Yate's correction, significant at P≤0.001)

***Tab. 2*** *– Confronto tra le comparse dei sintomi primari di* P. viticola *osservate nei vigneti della Tab. 1 e le comparse simulate dal modello ($\chi^2$ = 373.6, con la correzione di Yate, significativo per P≤0.001)*

| | | ***Observed*** | |
|---|---|---|---|
| | | No | Yes |
| Simulated | ***No*** | 414<br>*76,1%* | 0<br>*0%* |
| | Yes | 33<br>*6,1%* | 97<br>*17,8%* |

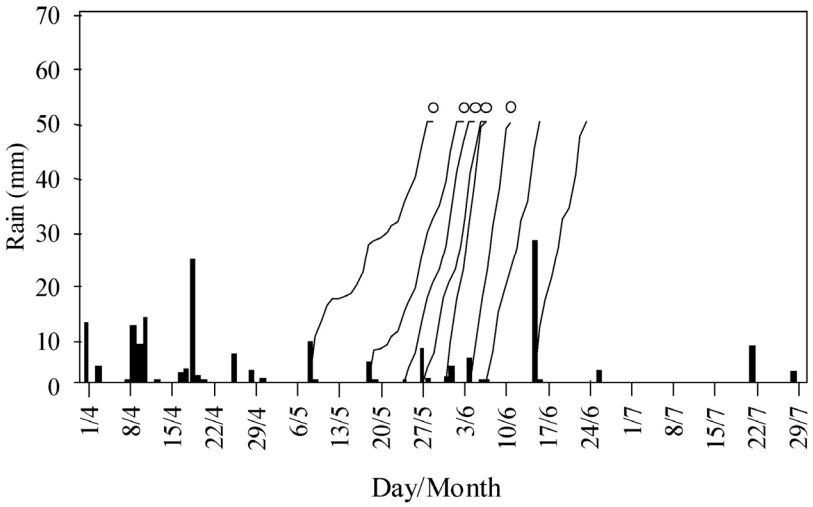


**Fig. 5** - Model simulations for Alba (Cuneo), in 2003. The model estimated the end of oospore latency on May 3. First simulation started on May 10 and afterwards the model ran seven simulations; six of them aborted before zoospore dispersal, while the last two simulations were interrupted before zoospore ejection. The model never simulated a complete infection cycle, and the disease never appeared during field observation for the entire season

***Fig. 5*** *– Simulazioni fornite dal modello ad Alba (Cuneo) nel 2003. Il modello ha stimato il superamento della latenza il 3 maggio. La prima simulazione è iniziata con la pioggia del 10 maggio e, in seguito, il modello ha effettuato sette simulazioni: sei sono state interrotte prima della diffusione delle zoospore, mentre le ultime due sono state interrotte prima del rilascio delle zoospore. Il modello non ha mai simulato un ciclo completo di infezione e la malattia non è mai comparsa nei rilievi di campo, durante tutta la stagione*

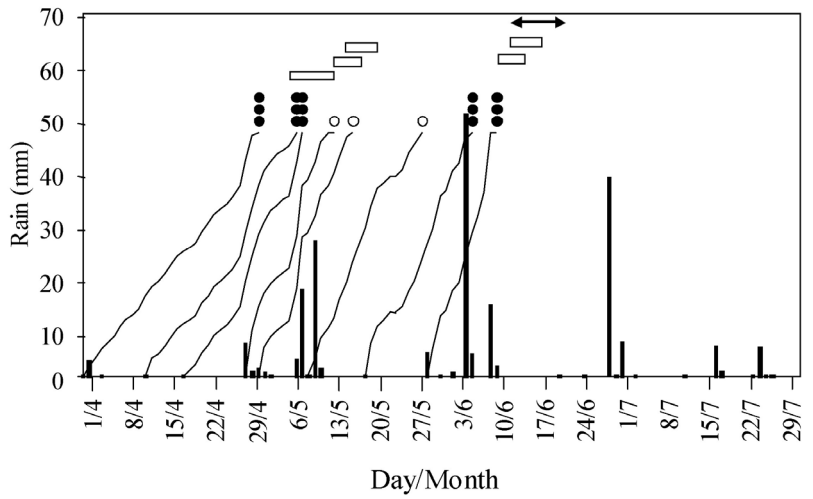


**Fig. 6** – Model simulations for S. Agata (Ravenna), in 1997. The model estimated the end of oospore latency on March 26; it provided three simulations that originated successful infections, whose symptoms are expected to appear between May 5 and 15. Actually, no disease appeared in such a period, so that the three simulations produced unjustified alarms. After three aborted simulations, the model provided two further successful infections and estimate symptoms appearance between June 7 and 13; actual downy mildew onset occurred between June 10 and 17

***Fig. 6*** *– Simulazioni fornite dal modello a S. Agata sul Santerno (Ravenna) nel 1997. Il modello ha simulato il superamento della latenza il 26 marzo; dopodiché ha fornito tre simulazioni che hanno originato infezione, la cui comparsa dei sintomi è stata prevista tra il 5 e il 15 maggio. Nessuna comparsa di sintomi è stata registrata in questo periodo di tempo; queste tre simulazioni hanno, quindi, generato allarmi ingiustificati. Dopo tre successive simulazioni interrotte, il modello ha poi prodotto ulteriori due simulazioni complete del ciclo di infezione, che hanno previsto una comparsa tra il 7 e il 13 giugno; la reale comparsa dei sintomi in campo è stata osservata tra il 10 e il 17 giugno*

not conducive for zoospore dispersal. The simulation initiated by rain occurred on May 31 ended with a successful infection on June 19, with an expected appearance of symptoms between June 25 and 28. First downy mildew symptoms were observed in vineyard on June 25.

At Alba (Cuneo), in 2003 (Fig. 5), the model simulated the end of oospore latency on May 3. First simulation started on May 10 and seven simulations were produced farther; six of them aborted before zoospore dispersal, while the last two simulations were interrupted before ejection of zoospores from zoosporangia. Therefore, the model never simulated a complete infection cycle, and the disease never appeared in the vineyard for the entire season.

The model produced some unjustified alarms due to overestimation of successful infections; in aggregate, there were 33 overestimations out of 544 cases (6%) (Tab. 2). A critical analysis of these cases showed that the level of rainfall triggering germination in the mature oospore cohorts is a possible cause for false positive simulations. The model assumes that 0.2 mm of rainfall are sufficient to moisten the leaf litter and initiate the germination process. Perhaps, this amount of water is insufficient when the rainfall follows a dry period and the leaf litter has a very low water content. Another possible explanation for the model overestimations is related to the growth stage of vine shoots. The model does not incorporate the possibility of rejecting a successful infection when the vine is not in the susceptible stage of 5-6 leaves unfolded (10 cm shoot length). Actually, a many

of the false infections produced by the model occurred in the early season.

For instance, at S. Agata (Ravenna), in 1997 (Fig. 6), the model simulated oospore maturity on March 26. First to third oospore cohorts initiated germination with rainfalls occurred on April 1, 11 and 17. These simulations ended with successful infections on April 29, May 7 and 8, respectively, but no disease symptoms appeared in the vineyard until mid June. So, these three simulations were overestimated. Later, the model simulated correctly the two successful infections that coincided with actual appearance of downy mildew in field. On April 1, the amount of rainfall was 2.9 mm and it surely moistened the leaf litter in a sufficient way to trigger germination. This infection process ended on April 29, when zoospores found favorable conditions for infecting leaves (7 hours of wetness with average temperature of 13.5°C). However, downy mildew did not appear. It is possible that, on April 29, leaves were not susceptible to infection, since the susceptible stage usually occurs within the first ten days of May. On April 11 and 17, the amount of rainfall was 0.2 mm, and in both cases the rainfall was preceded by some days with very low relative humidity. Therefore, it is possible that this few amount of rainfall did not allow a sufficient and homogeneous moistening of the leaf litter to trigger oospore germination.

## Conclusions

The dynamic model for primary infections caused by *P. viticola* on grape proved to be accurate and robust. In 94% of the simulations performed, the model correctly simulated primary infections; in the remaining 6% of cases, the model simulated an infection that did not actually occur. The model never failed to simulate actual infections.

The model was able to simulate primary infections in different epidemiological conditions, due to geographical position of vineyards, vine varieties and period of infection, from early to late disease onset.

Inaccuracies produced by the model were always due to false positive infections, which have a low negative impact on the model performances. Nevertheless, the model can be improved to further reduce false positive prognoses.

The model has a time step of one hour; therefore it makes the understanding of the infection progress possible with a high degree of detail.

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