Asian Journal of Mycology 7(2): 37–50 (2024) ISSN 2651-1339
www.asianjournalofmycology.org
Article
Doi 10.5943/ajom/7/2/4

Biology, diversity, detection and management of *Plasmopara viticola* causing downy mildew of grapevine (*Vitis* spp.)

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Rhouma A, Hajji-Hedfi L, Atallaoui K, Chihani-Hammas N, Godwin Okon O. 2024 – Biology, diversity, detection and management of *Plasmopara viticola* causing downy mildew of grapevine (*Vitis* spp.). Asian Journal of Mycology 7(2), 37–50, Doi 10.5943/ajom/7/2/4

Abstract

Grapevine downy mildew is a devastating disease that wreaks havoc on grapevines (*Vitis vinifera* L.) worldwide. The causal organism of this disease is *Plasmopara viticola*, a diploid obligate biotrophic oomycete native to North America. This pathogen has swiftly spread to grape-growing regions across the globe, particularly those blessed with warm, humid climates. *Plasmopara viticola* possesses a flexible mating system, employing both sexual and asexual means to propagate its lineage. *Plasmopara viticola* life cycle involves the production and dispersal of zoospores for grapevine infection. Zoospores produced within sporangia are released by rain or wind and swim in free water on the grapevine surface. They are attracted to stomata, where they encyst, germinate, and penetrate the host tissue. A substomatal vesicle develops, giving rise to intercellular mycelium. Under favorable conditions (warm, humid nights), sporulation occurs. Sporangiophores emerge through stomata, bearing sporangia that produce new zoospores. These zoospores are then dispersed by wind and rain to initiate new infection cycles on grapevine tissues. Meanwhile, *P. viticola*'s resilience is further enhanced by its ability to produce thick-walled oospores, which can overwinter in infected leaf debris, ready to unleash a fresh wave of destruction in the following spring. Downy mildew's destructive reach extends to all green tissues of grapevines, leaving a trail of devastation in its wake. Infection of leaves cripples photosynthetic efficiency, leading to a decline in grape quality. The infection of inflorescences and berries directly translates into yield losses. The current mainstay of downy mildew control is a heavy reliance on fungicide treatments. However, this approach is riddled with drawbacks, including exorbitant expenses, potential threats to human health, environmental contamination, and the inevitable emergence of fungicide resistance. In light of these shortcomings, researchers are actively exploring alternative, ecologically sound strategies to curb downy mildew's rampage, aiming to strike an integrated disease management balance between effective disease control and environmental stewardship. This comprehensive review provides in-depth insights into *P. viticola*, encompassing its taxonomy, host-pathogen interactions, symptoms, economic impact, epidemiology, distribution, infection mechanisms, and control strategies, with a strong focus on sustainable methods.

Submitted 15 Febuary 2024, Accepted 12 September 2024, Published 11 October 2024
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Keywords – downy mildew – grapevine – management practice – *Plasmopara viticola* – sustainability

Introduction

Grapevines, belonging to *Vitis* (*Vitaceae*), are widely cultivated crops with a rich history and global significance (Riaz et al. 2018, Grassi & De Lorenzis 2021, Sargolzaei et al. 2021). Originating in the Caucasian region, these plants have spread across the globe, occupying around 7.5 million hectares of land. Global grapevine cultivation achieved production of approximately 75 million tons in 2022, highlighting their adaptability and agricultural importance (FAO 2023). Grapevine cultivation has been an integral part of Tunisian agricultural heritage since the medieval era, with vineyards flourishing across diverse climatic and soil conditions. In 2016, grapevine production in Tunisia reached an impressive 133,500 tons, highlighting its significant contribution to the national socioeconomic fabric (DGEDA 2017, OIV 2019). This enduring legacy of grapevine cultivation underscores the resilience and adaptability of these remarkable plants, which have become deeply embedded in Tunisia's cultural landscape (Habib et al. 2020, Rhouma et al. 2021a, b).

Plasmopara viticola (Berk. & M. A. Curtis, Berl. & De Toni), the causal agent of grapevine downy mildew, stands as one of the most devastating pathogens plaguing viticulture globally (Clippinger et al. 2024). Since its identification in the mid-19th century, this disease has spread from its American origins to Europe and subsequently to every grape-growing region worldwide, inflicting substantial economic losses due to the scarcity of effective control measures (Koledenkova et al. 2022).

Copper sulfate was used to suppress a wide range of plant pathogens in 1885 and remains the most effective fungicide for controlling downy mildews. Throughout the 20th century, researchers developed contact and penetrating single-site fungicides for use against plant pathogens, including downy mildews (La Torre et al. 2019). However, the widespread use of these fungicides led to the emergence of resistant strains of the pathogen, rendering these treatments ineffective. Furthermore, due to the growing concerns about the negative environmental impact of chemical pesticides, the European Union imposed restrictions on their use (Llamazares et al. 2022). This prompted a surge in research efforts to develop alternative control strategies, such as breeding resistant grapevine cultivars, identifying new active ingredients, exploring natural products, and utilizing biocontrol agents. These alternatives can be applied individually or in combination to control the pathogen or mitigate its detrimental effects (Antoszewski et al. 2022, Mesguida et al. 2023, Rhouma et al. 2023, 2024a, 2024b).

This comprehensive review delves into *Plasmopara viticola*, providing in-depth insights into its taxonomy, host-pathogen interactions, symptoms, economic significance, epidemiological patterns, geographical distribution, infection mechanisms, and control strategies, with a particular emphasis on sustainable methods.

Etiology

Plasmopara viticola is a well-studied oomycete pathogen responsible for causing downy mildew in grapevines (*Vitis* spp.). Taxonomy and genetic variation of *P. viticola* are of great interest to researchers and grape growers in understanding the pathogen biology and evolution to develop effective management strategies (Yu et al. 2022). Here's an overview of the taxonomy and genetic variation of *P. viticola*.

Taxonomy

Plasmopara viticola (Berk. & M. A. Curtis) Berlese & De Toni (1888) belongs to *Peronosporaceae* in *Peronosporales*. This species was first collected by an American botanist and mycologist, Lewis David de Schweinitz, in 1834, and it was first named '*Botrytiscana*'. The fungal pathogen responsible for grapevine downy mildew has undergone several taxonomic revisions throughout history. Initially, this species was classified as *Botrytis cana* in 1848 by Ravenel and Berkeley, and it was subsequently reclassified as *Botrytis viticola* (Hendrickx 1948). In 1863, De

Bary provided a detailed description of its reproductive cycle and placed it in the genus *Peronospora* as *P. viticola* (De Bary 1863). Schröter (1886) later identified morphological and physiological differences within the *Peronospora* genus, leading to the establishment of a new genus named *Plasmopara*. Following this revised classification system, Berlese and De Toni assigned the pathogen its current taxonomic designation, *P. viticola*, in 1888 (Berlese & De Toni 1888). The currently accepted classification of *Plasmopara viticola* is Chromista, Oomycota, Oomycetes, Peronosporales, *Peronosporaceae*, *Plasmopara* (Gaforio et al. 2015, Fontaine et al. 2021, Koledenkova et al. 2022).

Genetic variation

While North America serves as the likely origin of *P. viticola*, European grapevines remained free of this pathogen until its accidental introduction in 1878 (Kump et al. 2000). This introduction unleashed a widespread epidemic, causing substantial grape yield losses across Europe (Gaforio et al. 2015). This led to several scientific efforts to understand the genetic makeup of the newly introduced *P. viticola* population in Europe, which commenced in 1998. Pioneering research in Swiss vineyards utilized Random Amplified Polymorphic DNA (RAPD) markers to assess the genetic diversity (Toffolatti et al. 2020). Following this initial work, further investigations throughout Europe have primarily focused on two main approaches, RAPD markers and microsatellites and simple sequence repeats (SSR markers), to delve deeper into the genetic structure of this invasive pathogen population. These studies provide valuable insights into the population dynamics and potential adaptation of *P. viticola* within the European viticulture landscape (Rouxel et al. 2012, Fontaine et al. 2013, Stark-Urnau et al. 2015).

Plasmopara viticola exhibits genetic diversity, which is important for its ability to adapt to changing environmental conditions and host resistance mechanisms (Santos et al. 2020). Researchers have used various molecular markers, such as microsatellites (simple sequence repeats or SSRs) and DNA sequencing, to study the genetic diversity and population structure of *P. viticola* (Toffolatti et al. 2020). Studies have revealed different genetic populations or lineages of *P. viticola* (Mesguida et al. 2023). These populations can exhibit variations in terms of virulence, resistance to fungicides, and other traits. Genetic variation in *P. viticola* can also be linked to host specificity (Rouxel et al. 2012). Different strains or isolates of the pathogen may have preferences for specific grapevine varieties, potentially leading to differences in the disease severity (Gessler et al. 2011). Fontaine et al. (2021) conducted a study to elucidate the global dispersal patterns of *P. viticola*. The researchers employed mitochondrial gene sequences and microsatellite markers to analyze 2000 isolates collected from the world's major wine-producing regions (North America, Europe, China, South Africa, Australia, and Argentina). Their analysis suggests that Europe is the origin of *P. viticola* introductions worldwide. A specific genetic cluster of *P. viticola* sp. *aestivalis* wreaked havoc on European vineyards, and European populations of this pathogen subsequently became the source for secondary introductions in other continents like China, South Africa, and Australia. Interestingly, the population structure of *P. viticola* appears to differ in warmer climates compared to regions with more favorable conditions (Koopman et al. 2007, Yin et al. 2014, Zhang et al. 2017, Taylor et al. 2019, Fontaine et al. 2021). The study conducted in South Africa suggests that populations in warmer regions might experience bottlenecks during unfavorable climatic events, leading to strong selective pressure. These findings suggest that climate might play a role in shaping the population structure of *P. viticola* (Koopman et al. 2007). As grape growers and breeders deploy resistant grapevine varieties and use fungicides, *P. viticola* can evolve to overcome these measures (Santos et al. 2020). This evolution is driven by the selection of pathotypes that can successfully infect resistant hosts or tolerate fungicides. Therefore, monitoring genetic variation is crucial for adapting management strategies (Koledenkova et al. 2022). *Plasmopara viticola* can form thick-walled oospores, a sexual reproductive structure. These oospores can contribute to the pathogen's genetic diversity as they provide a mechanism for genetic recombination. Advances in genomics have allowed for the sequencing of the *P. viticola* genome. This has provided insights into the pathogen's genetic makeup, which can help researchers identify potential targets for disease management (Paris et al. 2016, Toffolatti et al. 2020).

Host range

Plasmopara viticola, the causal agent of downy mildew in grapevines, has a host range primarily limited to various species within *Vitis*, which includes cultivated grapevines as well as wild and ornamental species (Fontaine et al. 2021). The host range of *P. viticola* is relatively specific, but it can vary depending on environmental conditions, the presence of alternative hosts, and genetic diversity within the pathogen population. Grapes (54% of the total host range) represent the significant economic impact of downy mildews (Taibi et al. 2023).

Vitis vinifera: *Plasmopara viticola* is most commonly associated with *V. vinifera*, the species of grapevine that is widely cultivated for wine production and table grapes (Boso et al. 2011, Gaforio et al. 2015).

Vitis labrusca: American grape species, such as Concord and Niagara, are also susceptible to downy mildew, though they tend to have more resistance than *V. vinifera* (Boso et al. 2011, Gaforio et al. 2015).

Vitis aestivalis: This American grape species is found in the eastern United States and can be a host for *P. viticola* (Boso et al. 2011, Gaforioet al. 2015).

Vitis riparia: Another American grape species found in North America is also susceptible to downy mildew (Boso et al. 2011, Gaforio et al. 2015).

Vitis rupestris: This American grape species is grown for its rootstock properties and can serve as a host for the pathogen (Boso et al. 2011, Gaforio et al. 2015).

Vitis rotundifolia: Muscadine grapes, native to the southeastern United States, can also be affected by downy mildew (Boso et al. 2011, Gaforio et al. 2015).

The primary host for *P. viticola* is *V. vinifera*, and this pathogen can cause significant damage to wine and table grape production. While *P. viticola* primarily infects grapevines, it is generally not a pathogen of other unrelated plant species (Boso et al. 2011, Gaforio et al. 2015). The specificity of this pathogen to *Vitis* species distinguishes it from some other plant pathogens with broader host ranges (Askani et al. 2021). However, it's essential to monitor and manage the disease to prevent its spread within and between vineyards (Salcedo et al. 2021, Koledenkova et al. 2022).

Rouxel et al. (2013) identified four potentially host-specialized lineages within *P. viticola*; this study employed a broader approach to investigate cryptic species diversity. Utilizing a wider geographic sampling area and a more diverse range of host plants, the authors leveraged phylogenetic analysis of multiple unlinked genes to discriminate five distinct cryptic species of *P. viticola* in eastern North America. Sampling from *V. vulpina* vines significantly yielded a novel phylogenetic lineage, designated as *P. viticola* clade *vulpina* (Taylor et al. 2000). This clade exhibited substantial genetic divergence and no apparent gene flow with previously described *P. viticola* species. However, the authors acknowledge the need for cross-pathogenicity testing to definitively establish host specialization of *P. viticola* clade *vulpina* on *V. vulpina*, particularly given that Rouxel et al. (2014) demonstrated the ability of another *P. viticola* species (clade *vinifera*) to infect this host. These findings strongly support the concept that grapevine downy mildew is caused by a complex of at least five cryptic species within *P. viticola*. Furthermore, this study highlights the diversification of these cryptic species across the *Vitaceae* family (Rouxel et al. 2014).

A recent study using phylogenetic and morphological analyses identified a new downy mildew species, *Plasmopara muralis*, responsible for outbreaks of *Parthenocissus tricuspidata* (Japanese ivy) in Europe (Thines et al. 2010, 2011). This finding challenges the previous understanding of *P. viticola*, which was thought to infect both *P. quinquefolia* (Virginia creeper) in North America and *P. tricuspidata* in Europe. The genus *Parthenocissus* encompasses various species cultivated globally for ornamental purposes, with some originating in North America (e.g., *P. quinquefolia*) and others in Asia (e.g., *P. tricuspidata*) (Golovina 1955, Rouxel et al. 2013). This geographic distribution of *Parthenocissus* species leads to several possibilities regarding the current distribution of the downy mildew pathogen. One scenario suggests a North American origin for the pathogen, where it infects *P. quinquefolia* and acts as an invasive species on *P. tricuspidata* in Europe. Alternatively, an unidentified downy mildew species potentially present in Asia on *Parthenocissus* spp. might have spread to infect both *P. tricuspidata* in Europe and *P. quinquefolia* in North America. It is important to note that previous descriptions have documented various *P. viticola* strains on endemic Asian *Vitis* spp. However, due to the lack of distinct morphological characteristics, these classifications are not widely accepted and require confirmation through molecular phylogenetic investigations. Regardless of the origin and spread, further research is needed to understand why this downy mildew species remained undetected on *P. quinquefolia* in Europe and *P. tricuspidata* in North America. One possibility is mild symptoms caused by *Plasmopara* spp. on *Parthenocissus* spp. historically resulted in overlooking the pathogens on these specific hosts (Rouxel et al. 2013, Rouxel et al. 2014).

Symptomatology and disease progression

The symptoms of downy mildew on grapevines are characteristic and can vary in appearance depending on the severity of the infection and environmental conditions. The symptoms typically appear on various parts of the grapevine, including the leaves, fruit, and young shoots (Fontaine et al. 2021, Koledenkova et al. 2022).

Leaf symptoms: The initial symptoms on grapevine leaves are yellow to pale green lesions that often have an angular or blocky appearance. These lesions develop on the upper surface of the leaves. On the lower surface of the affected leaves, you can observe a downy, white to grayish growth, which consists of sporangiophores and sporangia. These structures give the disease its name, "downy mildew." In severe cases of downy mildew, the infection can lead to defoliation, where the grapevine loses a significant portion of its leaves. This can reduce the vine's ability to photosynthesize and produce energy, ultimately affecting fruit production. Downy mildew can also make the plant more susceptible to secondary infections, such as powdery mildew and gray mold, which can further impact the grapevine's health (Salcedo et al. 2021, Mijailovic et al. 2022, Taibi et al. 2023).

Fruit symptoms: The disease can also infect grape berries. Infected berries may develop light, yellow-green lesions, which can become necrotic (turn brown or black) as the disease progresses. The presence of downy mildew on grape berries can significantly reduce their quality and market value (Salcedo et al. 2021, Mijailovic et al. 2022, Taibi et al. 2023).

Shoot symptoms: Young shoots can also be infected. Symptoms include blister-like lesions on the surface of the shoot, which can later become necrotic. Severe infections on young shoots can lead to the distortion and deformation of the shoot, affecting its growth and vigor (Salcedo et al. 2021, Mijailovic et al. 2022, Taibi et al. 2023).

The development of these symptoms is influenced by environmental conditions, such as high humidity and moderate temperatures. Rainfall or dew on leaves provides the necessary moisture for the pathogen to sporulate and spread. As the disease progresses, the symptoms can intensify and lead to significant damage to grapevine crops (Fernandes de Oliveira et al. 2021, Yu et al. 2022).

Economic importance

Plasmopara viticola causes a major economic threat to the grape and wine industries. Downy mildew significantly reduces grape yields and fruit quality, leading to substantial financial losses for growers. Additionally, managing *P. viticola* infections necessitated increased production costs due to the implementation of fungicide applications and other control measures. Here are several key aspects of the economic importance of downy mildew (Eisenmann et al. 2023).

Downy mildew can cause a substantial reduction in grape yields. Infected grapevines may produce fewer and lower-quality grapes, leading to decreased crop yields (up to 80%). This directly affects the revenue of grape growers, especially in regions with high disease pressure (Velasquez-Camacho et al. 2023, Fabre et al. 2024, Roda et al. 2024).

In addition to reduced yields, downy mildew can affect the quality of grapes. Infected grapes may develop off-flavors and aromas, impacting the taste and market value of wine and other grape products. For wine producers, the quality of the grapes is of utmost importance. Downy mildew can reduce the quality of grapes, affecting the flavor, aroma, and overall characteristics of the wine. This can result in lower-quality wines or the need for additional processing steps, further increasing production costs. Decreased grape quality and yield can lead to lower revenue for wineries and vineyard owners. High-quality grapes are essential for producing premium wines, which can command higher prices in the market (Koledenkova et al. 2022, Mijailovic et al. 2022, Taibi et al. 2023).

To control downy mildew, grape growers often need to invest in fungicides and other disease management measures. These costs can add up, especially in vineyards with recurrent disease problems. Over-reliance on fungicides to manage downy mildew can lead to the development of fungicide-resistant strains of the pathogen. When this happens, grape growers may need to use more expensive or less effective fungicides, increasing their production costs. Managing downy mildew requires additional labor for activities like scouting, spraying fungicides, and other disease control practices. Increased labor costs can be a significant economic burden for grape growers (Koledenkova et al. 2022, Llamazares et al. 2022).

The viticulture industry invests in research and development to improve disease management strategies and develop new resistant grape varieties. These research efforts require funding and resources (Koledenkova et al. 2022, Yu et al. 2022, Taibi et al. 2023).

Downy mildew is not limited to specific regions, and it can affect grape production around the world. Its economic impact is felt by grape growers, wineries, and related industries on a global scale (Eisenmann et al. 2023, Velasquez-Camacho et al. 2023).

Factors affecting the epidemiology

The epidemiology of *P. viticola* is influenced by various factors that affect the disease's occurrence, spread, and impact. Understanding these factors is crucial for managing the disease effectively (Koledenkova et al. 2022).

Environmental factors: High humidity and moisture, often associated with rainfall or dew, create favorable conditions for the pathogen's sporulation and infection. The presence of free moisture on grapevine leaves is essential for spore germination and disease development. Moderate temperatures between 15–25°C are conducive to downy mildew development. Warmer temperatures can speed up the disease cycle, while colder temperatures can slow it down. Seasonal changes, including spring and early summer rains, can affect the timing and intensity of downy mildew outbreaks (Fernandes de Oliveira et al. 2021, Yu et al. 2022).

Host susceptibility and resistance: The susceptibility of grapevine varieties to downy mildew varies. Some grapevine varieties are more resistant to the pathogen, while others are highly susceptible. Planting resistant varieties can reduce disease incidence (Boso et al. 2011, Gaforio et al. 2015).

Cultural practices: Pruning and canopy management practices can influence the microclimate within the grapevine canopy, affecting disease development. Proper pruning can improve air circulation, reduce humidity, and limit disease pressure. The layout and spacing of grapevines in the vineyard can impact air movement and sunlight exposure, which can, in turn, affect disease development (Fernandes de Oliveira et al. 2021, Mesguida et al. 2023).

Fungicide application: The application of fungicides is a common practice for managing downy mildew. The choice of fungicides, timing of applications, and resistance management strategies can influence the effectiveness of disease control (La Torre et al. 2019, Rhouma et al. 2021b).

Inoculum sources: The presence of overwintering oospores in plant debris and fallen leaves from the previous growing season can serve as a source of primary inoculum for disease development in the spring. The presence of wild *Vitis* spp. or other susceptible plants in the vicinity can provide a source of inoculum for *P. viticola* (Yu et al. 2022).

Monitoring and early detection: Regular scouting and monitoring for disease symptoms are crucial for early detection. Early intervention can help reduce disease spread (Hasanaliyeva et al. 2022).

Geographic location: The disease's prevalence and severity can vary by geographic location. Regions with a climate conducive to downy mildew development may experience more frequent and severe outbreaks (Fontaine et al. 2021).

Understanding these factors and their interactions is essential for developing comprehensive strategies to manage downy mildew in grapevines. Proactive and integrated disease management practices that consider these factors can help mitigate the impact of the disease on grape production (Billar de Almeida et al. 2020, De La Huerta-Bengoechea et al. 2022).

Occurrence of *Plasmoparaviticola* worldwide

Plasmopara viticola is an airborne pathogen that has a global distribution, but its occurrence is influenced by environmental conditions and the presence of grapevine hosts. The disease is most common in regions with temperate and humid climates. Here's an overview of the geographical distribution of *P. viticola* worldwide. It's worth noting that while downy mildew can be found in various grape-growing regions around the world, its severity and prevalence can vary from year to year, depending on local climatic conditions and the effectiveness of disease management practices (Fontaine et al. 2021).

Downy mildew is believed to have originated in Europe, and it has been a significant problem in European vineyards for centuries. Regions like France, Italy, Spain, Germany, and Hungary are well-known for their grape cultivation and have a history of dealing with this disease. Downy mildew is also prevalent in North American vineyards, particularly in the eastern United States and Canada. American grape species, such as *V. labrusca* and *V. aestivalis*, can be affected by the pathogen. Countries in South America, including Argentina and Chile, are known for their grape production and have had to contend with downy mildew as well. In Australia and New Zealand, grapevines are cultivated, and downy mildew can be a concern, particularly in regions with suitable climates. Grapevines are in cultivated parts of Asia, such as China, India, and Japan. The environmental conditions are susceptible to downy mildew. Some regions in Africa, such as South Africa, Tunisia, and Morocco, have vineyards where downy mildew is a potential issue (Koledenkova et al. 2022).

Disease cycle

The disease cycle of *P. viticola* is a complex and well-defined process that involves several stages. Understanding the disease cycle is essential for implementing effective control measures (Figure 1) (Gessler et al. 2011, Fontaine et al. 2021, Yu et al. 2022).

Overwintering stage: The disease cycle begins with the overwintering stage. During the fall, the pathogen, in response to decreasing temperatures, forms thick-walled oospores within infected grapevine tissues, such as fallen leaves and woody debris. These oospores are survival structures capable of enduring adverse conditions (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Spring infection: With the arrival of spring, environmental conditions become more favorable for disease development. As temperatures rise and humidity increases, the oospores within overwintered plant debris begin to germinate (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Primary infection: The primary infection occurs when the oospores produce sporangia in response to rain or dew. These sporangia are released into the air and are carried by wind or rain to grapevine leaves and shoots (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Germination and infection: When sporangia land on the grapevine, they germinate to form motile zoospores, which swim in water films on the leaf surface. Zoospores enter the stomata (tiny openings) on the leaf's underside and establish infections in the plant tissues (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Symptom development: After infection, the pathogen grows within the grapevine tissues, causing the typical symptoms of downy mildew. This includes the appearance of angular yellow lesions on the upper leaf surface and a downy white to grayish growth on the lower leaf surface. The pathogen can also infect other green parts of the grapevine, including young shoots and fruit (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Secondary infections: As the disease progresses, the pathogen produces sporangia on the undersides of infected leaves. These sporangia are released into the air and can initiate secondary infections on other grapevine tissues (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Continued sporulation and spread: The cycle of sporulation, release, and infection can repeat multiple times during the growing season, especially when environmental conditions, such as high humidity and moderate temperatures, are conducive to disease development (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Late season sporulation: As the growing season progresses, the pathogen can produce a large number of sporangia, leading to an increase in disease pressure. This can lead to defoliation, affecting the grapevine's photosynthetic capacity and reducing fruit quality (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

Overwintering structures formation: Toward the end of the growing season, as environmental conditions become less favorable, the pathogen produces thick-walled oospores within infected grapevine tissues, completing the disease cycle. These oospores overwinter and serve as the primary source of inoculum for the following spring (Figure 1) (Koledenkova et al. 2022, Velasquez-Camacho et al. 2023).

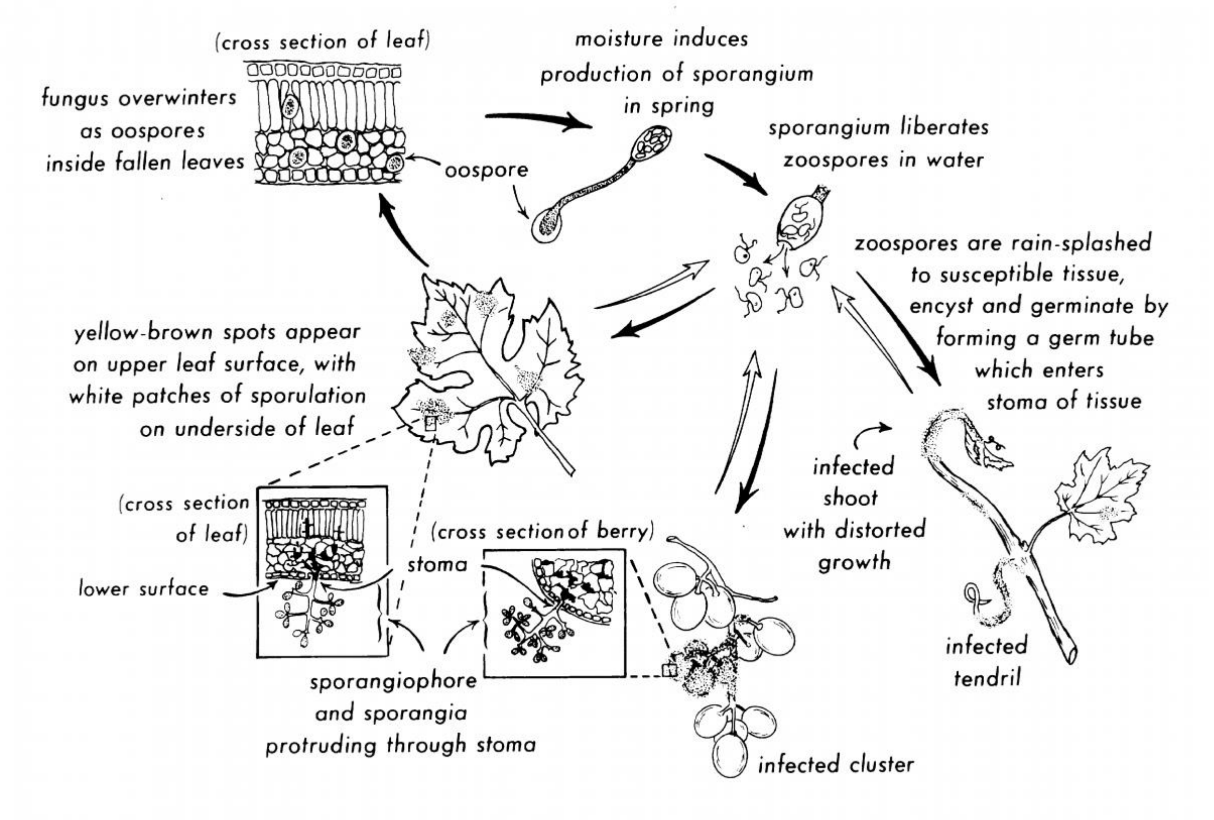

Fig. 1 – Disease cycle of downy mildew caused by *Plasmopara viticola* (Redrawn from Velasquez-Camacho et al. 2023)

Disease management

Despite providing a considerable level of protection against harmful plant diseases, chemical control methods face several challenges. Firstly, oomycetes invade leaf tissues through the formation of hyphae and haustoria, specialized structures that penetrate and extract nutrients from plant cells (Fernandes de Oliveira et al. 2021). Many fungicides, particularly contact types, primarily accumulate on and within the waxy cuticle layer of plant surfaces, failing to reach the deeper layers where these pathogens reside. Additionally, oomycetes can persist in soil and fallen leaves for extended periods, necessitating multiple fungicide applications to maintain control (Rhouma et al. 2021b, Rhouma et al. 2023). Furthermore, chemical control methods raise concerns regarding potential harm to human health and the environment. The development of acquired fungicide resistance in oomycetes and the emergence of new pesticide-resistant strains remain ongoing challenges that threaten the effectiveness of chemical control strategies (Rhouma et al. 2023).

The susceptibility of various grapevine cultivars to downy mildew was investigated using a combination of the leaf disc technique and field assessments of naturally infected plants. The findings revealed a spectrum of resistance levels, ranging from very low to very high. As anticipated for *V. vinifera* varieties, the majority of the cultivars demonstrated a high degree of susceptibility. Interestingly, select cultivars, primarily those originating from humid temperate regions of Spain, exhibited a remarkable level of resistance. These resistant cultivars include Sousón, Beltza, Hondarrabi, Folle Blanch, Ferrón, and Caiño Tinto (Boso et al. 2011, Gaforio et al. 2015).

Grapevines harbor a vast community of microorganisms, including epiphytes, endophytes, and rhizosphere inhabitants (Antoszewski et al. 2022). Biological control, an eco-friendly approach to plant disease management, utilizes beneficial fungi and bacteria to suppress plant pathogens. This strategy offers an environmentally sustainable alternative to conventional chemical pesticides and can be integrated into broader pest management systems (Billar de Almeida et al. 2020, De La Huerta-Bengoechea et al. 2022).

Endophytic fungi *Acremonium persicinum* and *A. sclerotigenum* exhibited hyperparasitism against *P. viticola*. Their culture filtrates, crude extracts, secondary metabolites, and acremines inhibited sporangial germination of the pathogen in anti-germinative assays (Billar de Almeida et al. 2020). Leaf disk studies revealed significant inhibition of asexual reproduction; sporangiophores were thin, deformed, and only grew at inoculation sites. Pre-infection foliar application of crude extracts from *Penicillium chrysogenum* and *Phomopsis* sp. effectively protected grapevine plants against natural infection in both greenhouse and field trials. *Trichoderma* spp. enhanced grapevine defenses against downy mildew in both induced and natural infection scenarios. They upregulated defense-related genes, primed plants for enhanced gene expression, and induced protective enzymes, leading to systemic resistance. *Trichoderma* spp. treatment also increased plant peroxidase levels and reduced disease severity after natural infection. The high cellulase production of *Trichoderma* spp. is likely involved in pathogen suppression (Kulišová et al. 2021, Mesguida et al. 2023, Rhouma et al. 2024a).

Pre-infection application with *Bacillus subtilis*, *B. pumilus*, *Pseudomonas fluorescens*, *Streptomyces atratus*, *Paenibacillus* spp., and *Ochrobactrum* spp. induced systemic resistance in greenhouse-grown plants, reducing downy mildew disease severity and increasing polyphenol oxidase levels. These bacteria also improved plant growth parameters, yield, and chemical composition (Vandana et al. 2021, Antoszewski et al. 2022, Boiu-Sicuiaet al. 2023, Rhouma et al. 2024b).

Despite their promising potential as eco-friendly alternatives to synthetic pesticides, plant-derived products (PDPs) face several challenges that hinder their widespread adoption in commercial agriculture (Okon et al. 2023). While PDPs extracted from various plant sources have demonstrated efficacy against a range of pests and diseases under controlled laboratory conditions, their performance in field settings often falls short of expectations (Matrood & Rhouma 2021). This discrepancy is primarily attributed to the high water solubility of PDPs, which causes them to wash off easily with rainfall, reducing their effectiveness and necessitating frequent reapplications (Matrood & Rhouma 2021, Okon et al. 2023).

Under both field and greenhouse conditions, extracts of *Yucca schidigera*, *Quillaja saponaria*, *Larix decidua*, *Inula viscosa*, *Glycyrrhiza glabra*, *Frangula alnus*, and *Equisetum arvense* have demonstrated efficacy in controlling *P. viticola*. Extracts and essential plant oils of *Eucalyptus globulus*, *Solidago virgaurea*, *Thymbra spicata*, *Salvia officinalis*, *Citrus* spp., *Rheum palmatum*, *R. rhabarbarum*, *Origanum vulgare*, *O. majorana*, *Magnolia officinalis*, *Mentha piperita*, *Juncus effusus*, *Melaleuca alternifolia*, *Cinnamomum zeylanicum*, *Abies sibirica*, and *Cymbopogon citratus*, have shown promising results under semi-controlled conditions, suggesting the need for further research to optimize their effectiveness under fields (De Oliveira Fialho et al. 2016, Mulholland et al. 2017, Thuerig et al. 2018, La Torre et al. 2019, Rienth et al. 2019, Hajji-Hedfi et al. 2023, 2024).

β-1,3-glucan laminarin effectively reduced *P. viticola* damage by stimulating plant defense responses. In leaf disk assays under semi-controlled conditions and field trials with surfactant application, laminarin triggered the production of hydrogen peroxide at infection sites, activated defense gene expression, promoted callose and phenol deposition, and induced HR-like cell death, all of which contributed to enhanced disease resistance (Gauthier et al. 2014, Paris et al. 2016).

Conflicts of interest

The authors declare that they have no conflict of interest. All authors have approved the manuscript for submission. The authors confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

Acknowledgements

This research was funded by the REVINE (Regenerative agricultural approaches to improve ecosystem services in Mediterranean vineyards) project, affiliated with the PRIMA program.

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