

STUDY OF DOWNY AND POWDERY MILDEW DISEASE RESISTANCE GENES IN GRAPEVINE (A REVIEW)

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Abstract. Grapevine (*Vitis vinifera* L.) is one of the world's most economically important fruit crops, supporting fresh consumption and a wide range of processed products, particularly wine. Global grape production is increasingly threatened by climate change-driven abiotic stresses and severe biotic constraints, among which downy mildew and powdery mildew are the most destructive diseases. This manuscript reviews current knowledge on grapevine-pathogen interactions with *Plasmopara viticola* and *Erysiphe necator*, focusing on disease symptoms, impacts on yield and fruit quality and underlying molecular mechanisms of host defense. We summarize major resistance loci, including *Rpv*, *Run* and *Ren* and highlight the roles of pathogen effectors, host immune signaling and metabolic reprogramming during infection. Advances in conventional breeding, introgression from wild *Vitis* species and modern biotechnological approaches such as CRISPR/Cas9-mediated genome editing and susceptibility gene targeting are discussed. Understanding these mechanisms provides a foundation for developing durable, disease-resistant grapevine cultivars under changing environmental conditions.

Keywords: Grapevine, downy mildew, powdery mildew, resistance genes.

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1. Introduction

Grapevine is one of the most economically valuable fruit crop worldwide, owing to the diverse range of products obtained from its cultivation. The largest contributors to global grape production include China, Italy, Spain, France and the United States, which together produce nearly 50% of the world's total output (Atak, 2022). Recent estimates show that vineyards occupy approximately 7.3 million hectares globally and generate around 77.8 million tons of grapes annually, supplying the wine sector as well as fresh-fruit and dried-fruit markets (Mammadova *et al.*, 2026; Salimov *et al.*, 2025a). Although grapes are well known for their pleasant flavor, only about 27% of total production is consumed fresh. The remaining portion is processed into various products, including raisins, juices, jellies and wines. Grape juice is typically produced from table grape varieties containing approximately 15% sugar by weight, whereas wine production relies primarily on wine grape cultivars, which are characterized by higher sugar concentrations, reaching nearly 24%. Globally, about 71% of harvested grapes are utilized by the wine industry, while only around 2% are processed into raisins through drying methods (Hussain *et al.*, 2021).

Azerbaijan is particularly rich in grapevine diversity, with more than 500 cultivars and viticulture represents a key component of the country's agricultural economy and social heritage (Alizada *et al.*, 2024; Salimov *et al.*, 2025b; Mammadova *et al.*, 2025). However, ongoing climate change has intensified both biotic and abiotic stresses, resulting in reduced yield and quality across many agricultural systems, including grape production (Alizada *et al.*, 2020; Alizada, 2022; Alizade & Mammadova, 2023).

In addition to climatic pressures, grapevine cultivation is severely constrained by numerous pathogens and pests. The crop is vulnerable to infections caused by fungi, bacteria and viruses, as well as damage from herbivorous organisms such as nematodes and phylloxera. To date, at least 267 disease-causing species belonging to 53 genera have been reported to affect grapevine roots, trunks, leaves and fruits. Among these, powdery mildew, downy mildew and gray mold are recognized as the most destructive diseases impacting grapevine production worldwide (Li *et al.*, 2025). Understanding their molecular interactions with grapevine hosts is therefore essential for developing durable resistance strategies.

2. Downy mildew

2.1. Pathogen biology and symptoms

Plasmopara viticola is an obligate biotrophic pathogen classified within the Oomycetes, order *Peronosporales* and family *Peronosporaceae* and it is specifically adapted to hosts of the family *Vitaceae*. This pathogen is capable of infecting all photosynthetically active tissues of grapevine. Initial symptoms on leaves typically appear as rounded, pale yellow, semi-transparent lesions commonly referred to as “oil spots,” reflecting olive-toned margins surrounding the affected areas. As disease severity increases, infected leaves undergo necrosis, turn brown and abscise prematurely. Reproductive organs, particularly inflorescences, are highly vulnerable; infection of young berries by sporangia often results in bunch rot characterized by grayish fungal growth (Viret & Gindro, 2025).

2.2. Breeding and biotechnological strategies

The development of grapevine cultivars with enhanced tolerance to biotic and abiotic stresses can be achieved through conventional breeding strategies, targeted hybridization with related species harboring natural resistance loci and modern genome-editing technologies (Akparov *et al.*, 2021; Alizade, 2022; Alizade *et al.*, 2023; Mammadova *et al.*, 2021; Zamanli *et al.*, 2025). Multiple genetic components involved in resistance to downy mildew have been identified in grapevine. For instance, the *P. viticola* Crinkler effector PvCRN17 interferes with Fe-S protein-dependent defense pathways by interacting with the grapevine protein VAE7L1, thereby impairing Fe-S cluster assembly and the maturation of Fe-S proteins (Xiang *et al.*, 2022). Similarly, the RxLR effectors RxLR31154 and RxLR50253 enhance host susceptibility by targeting and stabilizing the grapevine proteins VpPsbP and VpBPA1, respectively (Liu *et al.*, 2021; Yin *et al.*, 2022).

2.3. Resistance mechanisms and pathogen effectors

Resistance to downy mildew is governed by multilayered immune responses involving pathogen recognition, signaling cascades and metabolic reprogramming.

Pathogen effectors can either suppress or activate host immunity depending on their localization and host targets.

Beyond immune suppression, certain pathogen effectors can also activate host defense responses depending on their subcellular localization. The effector PvAVH53 translocates into the nucleus, where it interacts with grapevine importin- α proteins (VvImpas), known positive regulators of resistance, thereby triggering innate immune responses against downy mildew (Chen *et al.*, 2021). In contrast, PvCRN11-mediated resistance enhancement does not rely on nuclear localization but operates through a BAK1-dependent signaling pathway, leading to increased resistance (Fu *et al.*, 2023b). Notably, PvAvh77 exhibits dual functionality: it suppresses grapevine immunity when localized in the nucleus, yet elicits defense responses when acting in the apoplastic space (Fu *et al.*, 2023a; Li *et al.*, 2025).

Additional studies have demonstrated that overexpression of genes involved in periplasmic protein degradation, namely *VvDEG5* and *VvDEG8*, significantly enhances grapevine resistance to downy mildew (Fu *et al.*, 2024). Moreover, CRISPR/Cas9-mediated knockout of the susceptibility genes *VviDMR6-1* and *VviDMR6-2* has been shown to reduce host vulnerability to *P. viticola* infection (Giacomelli *et al.*, 2023).

2.4. Major resistance loci

Major resistance loci associated with downy mildew defense have been extensively investigated to elucidate the genetic architecture underlying durable host resistance. *Rpv3* has been identified as a major determinant of downy mildew resistance in numerous European grapevine cultivars. Resistance conferred by *Rpv3* is linked to the activation of stilbene biosynthesis and programmed cell death, which together restrict - but do not entirely prevent - pathogen proliferation. The presence of a tightly packed cluster of NB-LRR genes at the *Rpv3* locus provides a substantial adaptive advantage, particularly in native North American grapevine species that display strong tolerance to downy mildew (Eisenmann *et al.*, 2019; Di Gaspero *et al.*, 2012). Another important resistance locus *Rpv10*, represents a valuable genetic resource for breeding novel resistant cultivars (Schwander *et al.*, 2012; Zhang *et al.*, 2025).

However, resistance durability remains a challenge, as demonstrated by the recent breakdown of downy mildew resistance in the cultivar Bianca (Peressotti *et al.*, 2010; Merdinoglu *et al.*, 2018). The resistance of Bianca is primarily governed by the *Rpv3* locus (Bellin *et al.*, 2009), which provides partial protection against most *P. viticola* isolates. Nevertheless, infection with the highly virulent strain L, rendered Bianca as susceptible as the widely known susceptible cultivar Chardonnay (Peressotti *et al.*, 2010).

In summary, resistance to downy mildew relies on coordinated immune signaling, specialized resistance loci and emerging genome-editing tools. Durable protection will likely require pyramiding multiple loci together with susceptibility-gene modification to limit pathogen adaptation.

3. Powdery mildew

3.1. Pathogen biology and disease impact

Erysiphe necator is an obligate ectophytic fungus that colonizes the surface of grapevine green tissues and forms haustoria that penetrate epidermal cells to extract nutrients. The pathogen is capable of infecting all photosynthetically active organs of the

vine. Early disease symptoms are often subtle and difficult to distinguish, typically appearing as faint chlorotic areas on the upper leaf surface that may be mistaken for the initial stages of downy mildew. Corresponding lesions on the abaxial leaf surface become brownish-gray beneath the developing fungal mycelium. Powdery mildew can be observed throughout all stages of berry development, with young, actively growing tissues showing the highest susceptibility. As infection progresses, the fungus progressively damages and destroys the epidermal cells of affected berries (Viret & Gindro, 2025).

Beyond yield reduction, powdery mildew significantly compromises grape quality by modifying key biochemical traits, including sugar accumulation, organic acid composition and anthocyanin concentration (Calonnec *et al.*, 2004). These alterations negatively influence wine sensory properties, as documented by changes in aroma and flavor profiles (Lopez-Pinar *et al.*, 2017). Pigmentation is also affected, as reductions in anthocyanin levels lead to diminished color intensity in red wines (Amati *et al.*, 1996). Furthermore, *E. necator* infection induces extensive metabolic reprogramming in grapevine tissues. At the primary metabolism level, the abundance of proteins involved in glycolysis, photorespiration and photosynthesis is markedly reduced, reflecting a broad disruption of host physiological processes (Marsh *et al.*, 2010; Pimentel *et al.*, 2021).

3.2. Genetic basis of resistance

The genetic basis of resistance to powdery mildew involves a complex interplay of host defense genes, resistance loci and regulatory pathways that collectively determine the plant's ability to recognize and restrict pathogen development. Resistance to powdery mildew in the Vitaceae is mainly governed by two major gene families, designated *Run* (Resistance to *Uncinula necator*) and *Ren* (Resistance to *Erysiphe necator*). Numerous resistance loci have been identified across different Vitaceae species (Sosa-Zúñiga *et al.*, 2022). Prominent quantitative resistance loci include *Run1* on chromosome 12 (Barker *et al.*, 2005), *Ren4* on chromosome 18 (Mahanil *et al.*, 2012) and *Ren6* on chromosome 9 (Pap *et al.*, 2016). These loci originate from *Muscadinia rotundifolia*, *Vitis romanetii* and *V. piasezkii*, respectively and collectively confer strong resistance to powdery mildew (Cadle-Davidson, 2019).

Table 1. List of key resistance and susceptibility genes

Gene/Locus	Type	Origin	Resistance Effect
<i>Rpv3</i>	Resistance locus	North American Vitis	Partial resistance; induces stilbenes and HR
<i>Rpv10</i>	Resistance locus	<i>Vitis amurensis</i>	Strong quantitative resistance
<i>Run1</i>	Resistance locus	<i>Muscadinia rotundifolia</i>	Near-complete resistance
<i>Ren4</i>	Resistance locus	<i>Vitis romanetii</i>	Quantitative resistance
<i>Ren6</i>	Resistance locus	<i>Vitis piasezkii</i>	Broad resistance
<i>MLO genes</i>	Susceptibility genes	Conserved plant family	Knockout increases resistance
<i>DMR6</i>	Susceptibility gene	<i>Vitis vinifera</i>	Editing reduces infection

Massonnet *et al.* (2022) conducted a comparative analysis of powdery mildew defense responses in interspecific grapevine populations segregating for individual resistance loci derived from *M. rotundifolia* (*Run1*, *Run1.2b*, *Run2.1*, *Run2.2*), *V. cinerea* (*Ren2*), *V. romanetii* (*Ren4D* and *Ren4U*) and the hybrid cultivar Villard blanc (*Ren3*). Using a combination of microscopy, visual disease scoring and pathogen biomass

quantification, the authors demonstrated that these eight resistance loci restrict infection at distinct stages of pathogen development (Table 1). Transcriptomic comparisons revealed limited overlap among differentially expressed genes associated with each resistance locus, with nearly half of the identified genes being specific to a single locus. Notably, *Run1*, originating from *V. rotundifolia*, was shown to confer complete resistance to powdery mildew (Feechan *et al.*, 2015).

3.3. Breeding and biotechnological strategies

Modern breeding and biotechnological approaches play a crucial role in developing grapevine cultivars resilient to both biotic and abiotic stresses (Alizade, 2023; Alizada & Aliyeva, 2024; Alizada *et al.*, 2025). In addition to resistance genes, the identification and manipulation of susceptibility genes (S genes) has emerged as a promising strategy, as loss of S-gene function can lead to enhanced disease resistance. One well-characterized group of S genes is the *Mildew Locus O (MLO)* family, which is conserved across plant species. Functional disruption of specific *MLO* genes has been shown to increase resistance to powdery mildew. For example, silencing *VvMLO6*, *VvMLO11* or *VvMLO13* individually did not significantly affect disease severity, whereas simultaneous knockdown of *VvMLO7* together with *VvMLO6* and *VvMLO11* reduced powdery mildew symptoms by up to 77% (Pessina *et al.*, 2016).

Further evidence from genome-editing studies demonstrated that targeted modification of *VvMLO3/4* produced grapevine lines with contrasting phenotypes. While some edited lines exhibited normal growth, others developed senescence-like chlorosis and necrosis. Importantly, several *VvMLO3*-edited lines displayed enhanced resistance to powdery mildew, accompanied by host cell death, cell wall apposition and accumulation of hydrogen peroxide (Wan *et al.*, 2020). Additional regulatory components involved in powdery mildew defense have also been identified. Overexpression of *VvPUB26* in transgenic grapevines enhanced resistance, whereas disruption of this gene increased susceptibility to *E. necator* (Zhao *et al.*, 2024). Two calcium-dependent protein kinases, *VpCDPK9* and *VpCDPK13*, were shown to positively regulate salicylic acid and ethylene signaling pathways, thereby contributing to powdery mildew resistance (Hu *et al.*, 2021). Moreover, loss-of-function mutants of *VvPR4b* exhibited increased susceptibility to downy mildew in leaf-disc assays (Li *et al.*, 2020).

Overall, powdery mildew resistance reflects interactions among major loci, signaling regulators and susceptibility factors. Integrating these components through breeding or genome engineering provides the most promising route toward stable resistance.

4. Conclusion

In conclusion, downy mildew and powdery mildew remain major threats to sustainable grapevine production, particularly under the increasing pressure of climate change. Significant progress has been made in understanding the complex interactions between grapevine and its pathogens *Plasmopara viticola* and *Erysiphe necator*, including the identification of key resistance loci, pathogen effectors and host defense pathways. The integration of classical breeding with genetic resources from wild *Vitis* species and modern biotechnological tools, such as genome editing and susceptibility gene manipulation, offers promising opportunities to enhance resistance durability. Future research should focus on combining multiple resistance mechanisms and

improving their stability across environments to ensure long-term protection. Such strategies are essential for maintaining grape yield, fruit quality and the economic sustainability of viticulture in a changing global climate.

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