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Biotic Stress Resistance in Grapevines: A Review of Defense Mechanisms and Breeding Strategies

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Abstract Studying the defense mechanisms and breeding strategies for grapevine resistance to biotic stresses is crucial for reducing pesticide use, enhancing yield stability, and promoting sustainable agricultural development. This study summarizes the primary defense mechanisms of grapevines against biotic stresses, including innate immune responses, specific immune responses, biochemical defenses, and physical barriers. It also reviews the application of traditional hybrid breeding, marker-assisted selection (MAS), genomic selection (GS), and CRISPR/Cas9 gene editing in improving grapevine resistance, and analyzes several successful case studies, such as the development of powdery mildew-resistant, phylloxera-resistant, and multi-resistant grapevine varieties. The findings illustrate the practical outcomes of resistance breeding in agriculture, emphasizing that grapevine resistance is regulated by a combination of biological mechanisms and environmental factors. Abiotic stresses (e.g., drought and heat) often interact with biotic stresses, further complicating resistance research. To address these challenges, future research directions include integrating multi-omics technologies, fostering international collaboration to share germplasm resources, and leveraging precision breeding technologies to enhance the efficiency of resistant variety development. This study provides comprehensive insights into grapevine resistance research and practices, offering significant implications for sustainable grape production and disease management.
Keywords Grapevine; Biotic stress; Resistance breeding; Defense mechanisms; Gene editing

1 Introduction

When it comes to grapes, the first thing that comes to mind is the sweet and sour table grapes or the mellow wine (Viret et al., 2018). This fruit is indeed not simple. It can be seen in almost all climate conditions, from hot southern Europe to cool North America. But then again, although grapes are highly adaptable, they are often troubled by various diseases-downy mildew and powdery mildew are not a joke. If you don't pay attention, the grape yield will be reduced or even lost.

In order to deal with these diseases, growers have put a lot of thought into it. Spraying pesticides is a routine operation, but everyone has a headache if too much pesticide is used (Zhu et al., 2012). It costs money and pollutes the environment. Interestingly, some grape varieties are naturally more disease-resistant, which has inspired researchers: if they can figure out the defense mechanism of these grapes and then "transplant" the disease resistance to other varieties through breeding, wouldn't it be killing two birds with one stone?

Now scientists are already doing work in this area, such as locating disease-resistant genes and studying defense response mechanisms. What's more exciting is that new technologies such as gene editing may bring breakthroughs (Louime et al., 2010). Of course, the road is still long, but at least the direction is clear-breeding disease-resistant varieties will not only make grapes less likely to get sick, but also reduce the use of pesticides, which is good for the environment and growers.

2 Common Types of Biotic Stresses in Grapes

2.1 Diseases

There are many problems in the process of grape cultivation, especially various diseases. When it comes to fungal diseases, powdery mildew is definitely a tough guy-this disease caused by *Erysiphe necator* is common in vineyards around the world (Possamai et al., 2021). Interestingly, this fungus is particularly "picky" and only loves living tissue. You will see the characteristic white powder on leaves, stems and fruits, especially in warm and humid seasons, and it spreads at an alarming rate (Gadoury et al., 2012; Weng et al., 2014). However, in terms of the degree of damage, gray mold is not much less, especially in rainy areas.

Speaking of gray mold, the pathogen *Botrytis cinerea* is much more cunning. It kills plant tissue first and then slowly eats it-a typical "carrion-eating" fungus. It is most dangerous when the fruit is about to mature, not only reducing production but also affecting quality (Kelloniemi et al., 2015). By the way, the Malviya et al. (2022) developed a powdery mildew severity scoring system, which is very helpful for breeding disease-resistant varieties (Figure 1). In addition to these, fungal diseases such as black rot are also a headache. Usually, they are prone to outbreaks when the weather is hot and humid. Now they are mainly dealt with by spraying pesticides and cultivating disease-resistant varieties (Qiu et al., 2015).

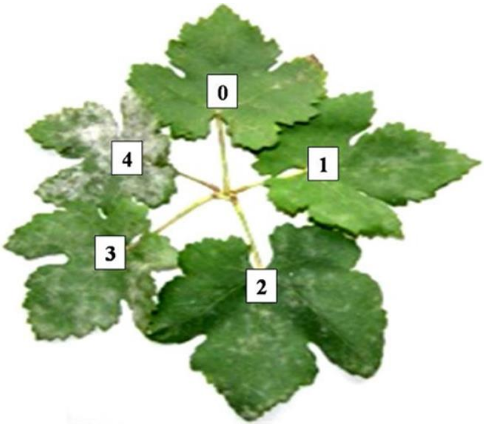

Figure 1 Pictorial depiction of 0~4 rating scale for powdery mildew disease severity (Adopted from Malviya et al., 2022)

2.2 Pests

Speaking of insect pests, phylloxera is a tough guy, specifically eating grape roots, and in severe cases, the entire plant will die. European grapes (*Vitis vinifera*) are particularly susceptible to the disease, and now resistant rootstocks are often used to prevent it (Fedorina et al., 2022).

2.3 Viral diseases

In terms of viral diseases, leaf curl virus is quite common. The leaves will change color and the quality of the fruit will deteriorate. It is mainly spread by mealybugs. There is also a red spot virus, which will cause red spots on the leaves and late ripening of the fruit. These two viruses cannot be cured now, and they mainly rely on controlling the spreading insects and cutting down the diseased plants (Fedorina et al., 2022). Massonnet et al (2022)'s study showed that poor management of these diseases can really seriously affect the harvest.

3 Defense Mechanisms of Grapes Against Biotic Stresses

3.1 Innate immune response

In fact, many plants have this ability-those special receptors (PRRs) on the surface of grape leaves can recognize the molecular characteristics of pathogens (PAMPs). Santos et al. (2020) conducted an experiment and found that when downy mildew was first infected, grapes would quickly adjust a bunch of defense-related proteins. However, this first line of defense (what experts call PTI) is sometimes not very reliable. For example, the Roatti et al. (2013) found that although the use of biological pesticides such as *Trichoderma* can strengthen defense, the effect is discounted when encountering drought or something.

3.2 Specific immune response

Speaking of this, we have to mention the R gene-equivalent to the "special forces" of grapes. Fröbel et al. (2019) found that grapes with the *Rpv10* gene would quickly activate dozens of defense genes when encountering downy mildew. Recently, Ricciardi et al. (2024) also found several new disease resistance gene clusters. Of course, scientists are not idle now. For example, the Capriotti et al. (2020) tried to use genetic modification technology to make these genes more active, but whether this method can be effective in the long run remains to be seen.

3.3 Biochemical defense

The phenolic substances in grape skins are not just for show. Maia et al. (2020) confirmed that these things can both strengthen cell walls and directly kill pathogens. Flavonoids are even more powerful. Ferrandino et al. (2023) found that it is not only antioxidant, but also "tip" other defense systems. What is particularly interesting is that gray mold and downy mildew actually trigger different chemical defenses-the former stimulates anthocyanin synthesis, while the latter mainly activates chalcone enzymes (Figure 2).

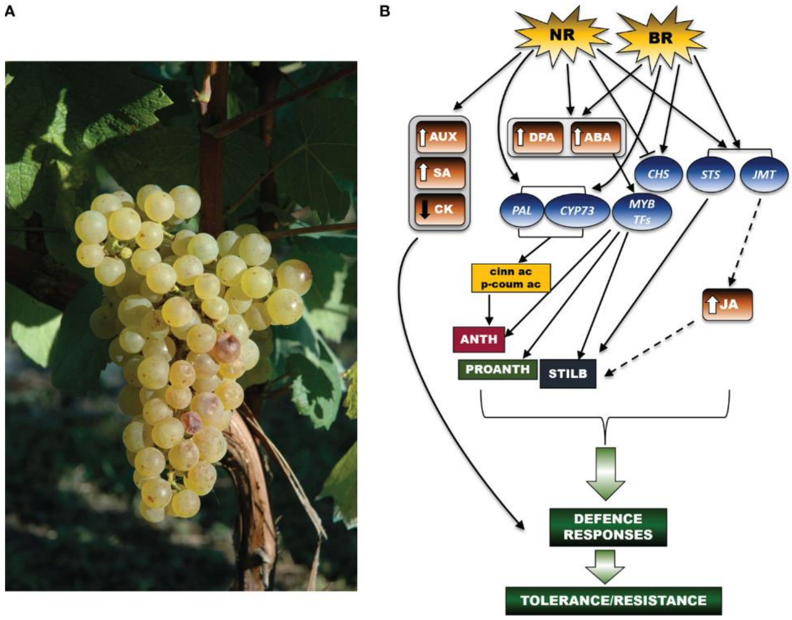

Figure 2 A schematic representation of the networks of hormonal and molecular signals regulating the secondary metabolism in the grapevine berry in response to *Botrytis cinerea* (Adopted from Ferrandino et al., 2023)

Image caption: (A) A grape bunch of *Vitis vinifera* cv Chardonnay showing very initial symptoms of *Botrytis cinerea* infection. (B) At the berry level, both NR (Noble Rot) and BR (Bunch Rot) infection induce an increase in DPA (dihydrophaseic acid) and ABA (abscisic acid) concentrations (Adopted from Ferrandino et al., 2023)

When it comes to enzymes, we have to mention two "model workers": peroxidase is responsible for cleaning up toxic oxides (Castro et al., 2023), and PAL enzyme is the "chief engineer" for synthesizing phenolic substances (Gauthier et al., 2014). They are like switches for the defense system, which can directly kill the enemy and activate systemic immunity.

3.4 Physical barriers

The wax on the surface of grapes is not just for looks. Ferrandino et al. (2014) pointed out that this layer of cuticle can both prevent bacteria and lock in moisture. If the bacteria force their way through, the grapes will urgently thicken the cell wall at the wound-the electron microscope photos taken by Santos et al. (2020) show that lignin will accumulate quickly at the infected site, just like cementing a city wall. However, this defense consumes a lot of energy, so it will only be activated when the bacteria are detected (Castro et al., 2023).

4 Strategies for Breeding Grapes Resistant to Biotic Stresses

4.1 Traditional breeding methods

You may not believe it, although molecular breeding is very popular now, traditional hybrid breeding is still very effective in the field of grape disease resistance. Take powdery mildew as an example. Researchers found that the *Run1* gene in wild grape *Muscadinia rotundifolia* and the *REN1* gene in cultivated grape *Vitis vinifera* are particularly effective. Putting these two genes together, the new varieties bred are extremely resistant to powdery mildew fungus *Erysiphe necator* (Agurto et al., 2017). However, it should be noted that this kind of gene stacking is not a simple matter, and it has to be done little by little through hybrid breeding. Merdinoglu et al. (2018) found that the reason why these new varieties are so powerful is that they can quickly produce disease-resistant substances and activate defense genes.

4.2 Molecular breeding technologies

Breeding is different now, with the magic tool of marker-assisted selection (MAS). In 2024, Ricciardi's team found that it was very fast to use it to find gene loci such as Rpv36 and Rpv37 that are resistant to downy mildew. But being fast is not enough. Genomic selection (GS) is more powerful and can deal with multiple traits at once (Fang, 2024). Dry et al. (2010) predicted that combining traditional breeding with these new technologies is the best way. For example, the project done by Qiu et al. (2015) proved that grapes bred in this way can resist several diseases at the same time.

4.3 Gene-editing technologies

The CRISPR/Cas9 technology, which has been very popular recently, has played a new trick in grape disease resistance. Wan et al. (2020) found that by cutting the *VvMLO3* gene, the resistance of grapes to powdery mildew increased. Interestingly, the grapes treated in this way grew quite normal. The principle is that the pathogens cannot find a breakthrough point to attack, and the grapes can also produce defensive substances themselves. However, the disadvantage is that the operation is more delicate and not every laboratory can do it.

4.4 Exploration and utilization of resistant germplasm resources

Did you know that many disease-resistant genes are actually "borrowed" from wild grapes. For example, against phylloxera, wild germplasm is a great savior. Agurto et al. (2017) conducted an interesting experiment: they combined the *Run1* of wild species with the *REN1* of cultivated species. As a result, the new variety cultivated had a particularly powerful defense system, which could produce a large amount of bactericidal substances and directly "starve" the bacteria to death. This also reminds us that it is really important to protect wild grape resources. Maybe one day we can find precious genes from them.

5 Interactions Between Grape Defense Mechanisms and the Environment

5.1 Combined effects of stresses

When it comes to the defense system of grapes, it is actually quite complicated. You may not know that grapes often have to deal with pests and diseases and weather changes in the field at the same time, and the two will affect each other. Take powdery mildew for example. Grapes are originally resistant to this disease, but the situation changes when they encounter high temperature and drought. Roatti et al. (2013) conducted an experimentand found that high temperature or drought alone is not a big deal, but if both come together, the disease resistance of grapes will be significantly reduced. This is mainly because the leaves lack water, causing some disease resistance genes to not work properly.

5.2 Relationship between diseases and climate change

Here is an interesting phenomenon: powdery mildew (caused by the fungus called *Erysiphe necator*) is more difficult to deal with under drought conditions. Zhou et al. (2024)'s study pointed out that drought can disrupt the hormone balance in plants, especially the two signaling pathways of salicylic acid and ethylene. You know, transcription factors such as VviWRKY10 and VviWRKY30 are supposed to help grapes resist powdery mildew, but once they encounter drought, they don't work well.

Climate warming is really a big problem now. As the weather becomes more unstable, pathogens like *Erysiphe necator* have a better life. Agurto et al. (2017) found that powdery mildew may become more common and more serious. Fortunately, scientists have found some disease-resistant genes, such as *Run1* and *REN1*. Combining these genes can make grapes more disease-resistant.

Speaking of future research directions, Liu et al. (2024) proposed that we must first understand how the grape defense system and environmental changes affect each other. The new disease-resistant gene loci found through GWAS technology are very helpful for breeding new varieties. As Ricciardi et al. (2024) said, if we can know the resistance genes for downy mildew and powdery mildew in advance, we can breed grape varieties that are more adaptable to climate change.

6 Successful Case Studies

6.1 Breeding of powdery mildew-resistant varieties

Due to the severe economic impact of powdery mildew (caused by *Erysiphe necator*), the development of powdery mildew resistant grape varieties has been an important research direction in the field of grape cultivation. The defense capabilities of grape varieties such as 'Crimson Seedless' were significantly enhanced through the stacking breeding strategy of resistance genes such as *Run1* and *REN1*. These hybrids exhibited strong resistance mechanisms, including reactive oxygen species (ROS) production and gene activation, which effectively prevented the establishment and growth of pathogens (Agurto et al., 2017). In addition, Wan et al. (2020) showed that the editing of the susceptible gene *VvMLO3* using CRISPR/Cas9 technology changed the growth characteristics of grape plants and their response to pathogen infection. Obvious trypan blue staining and H_2O_2 accumulation were observed in the mutant lines, indicating an enhanced cellular response to infection (Figure 3). The *VvMLO3* gene can play an important role in disease defense by regulating disease resistance-related signaling pathways in leaf cells, providing a new gene target for improving grape disease resistance, thereby obtaining grape lines with stronger resistance to powdery mildew, further demonstrating the potential of genetic engineering in breeding programs. The market performance of these hybrids is promising, as they provide long-lasting resistance without compromising grape quality and are an important resource for sustainable grape cultivation (Yu et al., 2024).

6.2 Development of grape phylloxera-resistant varieties

Grape phylloxera is a pest that damages grape roots and has traditionally been managed by using resistant rootstocks. Breeding programs have successfully utilized resistance genes naturally present in the American Vitis species to develop phylloxera-resistant grape varieties. These efforts have played a key role in maintaining grape production in areas severely infested with grape phylloxera. Integrating phylloxera-resistant genes into *Vitis vinifera* cultivars not only maintains the production of high-quality grapes, but also reduces dependence on chemical treatments.

6.3 Multi-resistant grape varieties

The development of grape varieties resistant to multiple diseases, such as powdery and downy mildew, requires the strategic stacking of resistance genes. For example, the PIWI grape variety was developed through traditional breeding methods with resistance to *Erysiphe necator* and *Plasmopara viticola*. These varieties are often bred by crossing with American or Asian grape varieties that carry natural resistance. Transcriptional analysis of these varieties revealed specific gene expression patterns that contribute to their disease resistance, providing important insights into the molecular mechanisms of multi-disease resistance (Scariolo et al., 2024). Such multi-resistant varieties are essential for sustainable grape cultivation as they reduce the need for chemical fungicides and improve the environmental and economic sustainability of grape production (Merdinoglu et al., 2018).

7 Current Challenges and Future Directions

7.1 Complexity of gene-environment interactions

When it comes to disease resistance in grapes, environmental factors are often a headache. Wang et al. (2023) found that rootstocks perform very differently in different places-some places can resist phylloxera, but in other places they may not even be able to resist nematodes. Of course, there are exceptions. For example, the Santos et al. (2020) noticed that some varieties have a relatively stable response to the *Plasmopara viticola* pathogen. In general, resistance genes are really difficult to control in a changing climate.

7.2 Limitations of germplasm resources

There are a lot of good things hidden in wild grape germplasm, as Ricciardi et al. (2024)'s recent studies have confirmed. But the reality is that the germplasm banks we have are really limited. Although in theory, protecting more genetic diversity can provide more options for breeding, such as the resistance traits discovered by Sargolzaei et al. (2020). But the problem is that it is not easy to collect and preserve so many resources in practice.

7.3 Technical challenges in biotic stress research

Nowadays, GWAS and transcriptome technologies have really helped a lot in grape disease resistance research. Fröbel et al. (2019) used these methods to find key resistance sites. But then again, these high-end technologies are both expensive and laborious. For example, Guan et al. (2018) mentioned that the interaction mechanisms between many pathogens and grapes are still unclear. Not to mention that some experiments are difficult to repeat, as Santos et al. (2020) has encountered before.

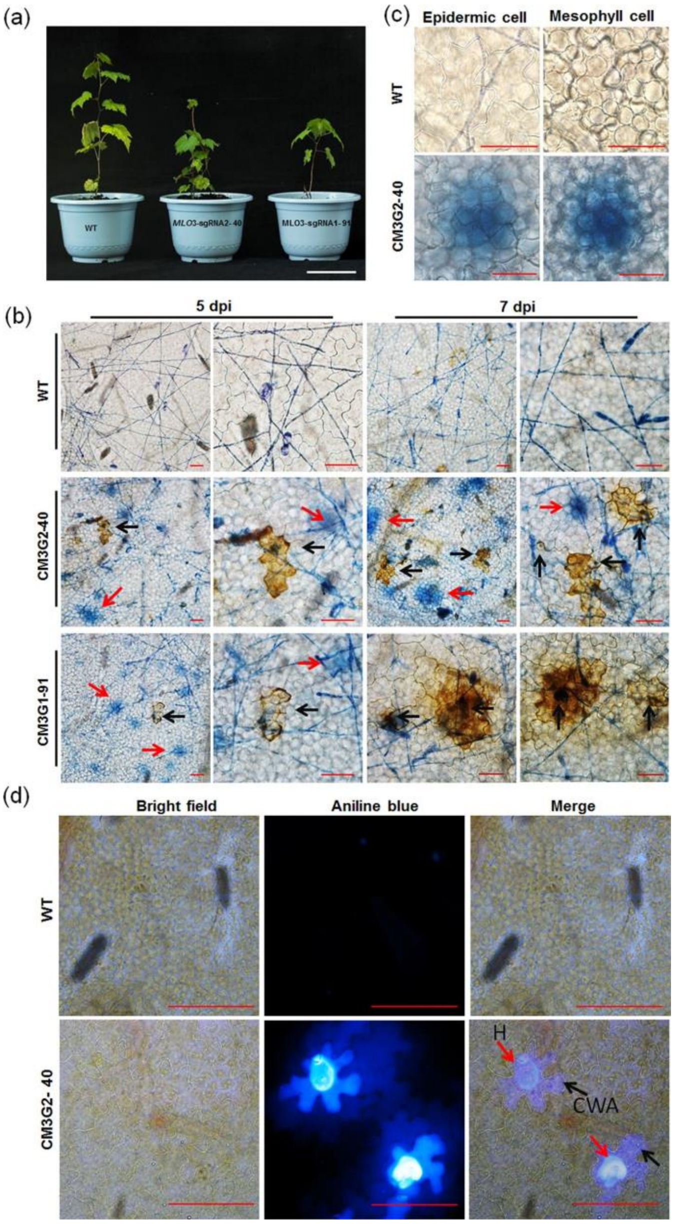

Figure 3 Analysis of the impact of *VvMLO3* gene editing on grapevine morphology and cellular disease resistance mechanisms (Adopted from Wan et al., 2020)

Image caption: a the wild-type (WT) and two *VvMLO3*-edited heterozygous mutant grapevine lines grown under phytotron conditions for 6 months (bar = 10 cm). b Representative micrographs showing DAB-and trypan blue-stained epidermal cells of the WT and *VvMLO3*-edited lines at 5 or 7 dpi. Red arrowheads indicate trypan blue retention, and black arrowheads indicate H_2O_2 accumulation (bar = 50 µm). c Representative images showing a trypan blue-stained leaf section of WT or CM3G2-40 with a focus on either the epidermal layer or the mesophyll cell layer at 7 dpi (bars = 50 µm). d Histochemical analysis of infection-triggered CWAs of epidermal cells of the WT and the heterozygous CM3G2-40 mutant line at 7 dpi. Red arrowheads indicate haustoria (H), and black arrowheads indicate infection-triggered CWAs (bars =50 µm) (Adopted from Wan et al., 2020)

7.4 Future research directions

Both Capriotti et al. (2020) and Guan et al. (2018) suggested integrating various omics data, which is a good idea. But this alone is not enough. After all, Pirrello et al. (2021) found that the data standards of different laboratories are not unified. So, we need to do more international cooperation in the future. The resource library project led by

Castro et al. (2023) is a good example. If everyone can share resistance resources in this way, the breeding progress will definitely be much faster. Of course, the premise is that countries are willing to truly open up resource exchanges.

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Conflict of Interest Disclosure
The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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