

Molecular Mechanisms of Tea Plant Resistance to Major Pathogens

Dandan Huang ✉

Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China

✉ Corresponding email: 3196820059@qq.com

Molecular Pathogens, 2024, Vol.15, No.1 doi: [10.5376/mp.2024.15.0004](https://doi.org/10.5376/mp.2024.15.0004)

Received: 06 Dec., 2023

Accepted: 20 Jan., 2024

Published: 09 Feb., 2024

Copyright © 2024 Huang, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Huang D.D., 2024, Molecular mechanisms of tea plant resistance to major pathogens, Molecular Pathogens, 15(1): 30-39 (doi: [10.5376/mp.2024.15.0004](https://doi.org/10.5376/mp.2024.15.0004))

Abstract Tea (*Camellia sinensis*) is an important beverage and cash crop in the world. Its disease resistance research is of great significance to the sustainable development of the global tea industry. This study outlines the main pathogen categories that affect tea trees and details the resistance (*R*) genes, pathogen recognition mechanisms and genetic maps in tea trees. The existence and function of resistance (*R*) genes play a central role in plant disease resistance. Through genomic analysis and quantitative trait locus (QTL) analysis, we have a deeper understanding of the genetic map of these *R* genes. The study of pathogen recognition mechanisms has also revealed a series of receptor proteins that can recognize pathogens and activate subsequent immune responses. This study also explores the interaction between pathogen effectors and host targets, the host's defense response, and how genome sequencing, CRISPR gene editing technology and transgenic methods are used to promote tea disease management, aiming to enhance tea disease resistance through scientific research and support the sustainable development of the global tea industry.

Keywords Tea plant disease resistance; Signaling pathways; Resistance genes; Secondary metabolites; Molecular interactions

1 Introduction

Tea (*Camellia sinensis*) is a globally significant crop, widely consumed as a beverage and valued for its economic importance. However, tea plants are susceptible to a variety of pathogens, which can severely impact yield and quality. Major diseases affecting tea plants include anthracnose, caused by *Colletotrichum* species, tea geometrid damage by *Ectropis oblique*, tea gray blight caused by *Pestalotiopsis theae*, and blister blight caused by *Exobasidium vexans* (Wang et al., 2015; 2018; Zhang et al., 2022). These diseases can lead to substantial crop losses, necessitating a deeper understanding of the molecular mechanisms underlying tea plant resistance.

Understanding the molecular mechanisms of plant resistance is crucial for developing effective strategies to combat these diseases. Resistance mechanisms in tea plants involve complex interactions between various signaling pathways, including those mediated by salicylic acid (SA), jasmonic acid (JA), and reactive oxygen species (ROS) (Wang et al., 2018; Jin et al., 2020; Liu et al., 2023a). Identifying key genes and pathways involved in these responses can inform breeding programs and genetic engineering efforts aimed at enhancing disease resistance in tea plants. For instance, the role of hypersensitive response (HR) and hydrogen peroxide (H₂O₂) accumulation in anthracnose resistance, and the involvement of specific genes like *CsUGT87E7* in SA metabolism, highlight the intricate defense strategies employed by tea plants (Jayaswall et al., 2016; Hu et al., 2021).

By synthesizing findings from recent transcriptomic, metabolomic, and microbiome studies, this study seeks to elucidate key signaling pathways and genes in tea plant defense against various pathogens, emphasize the role of phytohormones and secondary metabolites in mediating resistance, and discuss the potential application of these insights in developing disease-resistant tea varieties through breeding and biotechnological approaches. By achieving these goals, this study will contribute to a broader understanding of plant-pathogen interactions and support the development of sustainable disease management practices in tea cultivation.

2 Major Pathogens Affecting Tea Plants

2.1 Fungal pathogens

Fungal pathogens are among the most common and destructive agents affecting tea plants. One of the primary

fungal pathogens is *Colletotrichum camelliae*, which causes tea anthracnose, a disease that affects mature leaves and reduces both yield and quality. The cerato-platanin protein CcCp1 from *C. camelliae* plays a key role in fungal pathogenicity. Mutants lacking CcCp1 lose virulence and have a reduced ability to produce conidia, indicating the importance of this protein in the disease process. Additionally, the accumulation of jasmonic acid in susceptible tea cultivars upon infection suggests its role in regulating fungal infection (Liu et al., 2023b).

Another significant fungal pathogen is *Pestalotiopsis theae*, responsible for tea gray blight disease. Resistance to this pathogen has been linked to specific metabolites such as phenolic acids and flavonoids, which are more abundant in resistant tea plant resources. The presence of certain bacterial and fungal genera also correlates with resistance, highlighting the complex interplay between the tea plant's microbiome and its defense mechanisms (Zhang et al., 2022). Furthermore, the mycovirus *Pestalotiopsis theae* chrysovirus-1 (PtCV1) has been shown to modulate the pathogenic traits of *P. theae*, converting it from a virulent pathogen to a non-pathogenic endophyte, thereby providing an alternative approach to biological control (Zhou et al., 2021).

2.2 Bacterial pathogens

Bacterial pathogens also pose a significant threat to tea plants. The interaction between plants and bacterial pathogens involves complex genetic and molecular mechanisms. Plants have evolved resistance genes (*R* genes) that encode proteins capable of recognizing pathogen-derived molecules and triggering defense responses. These responses include the hypersensitive response (HR), which involves rapid tissue necrosis at the infection site to limit pathogen spread. The genetic basis of plant resistance to bacterial pathogens can be both qualitative and quantitative, involving major and minor genes, respectively (Zhang et al., 2013).

2.3 Viral pathogens

Viral pathogens are less common but can still cause significant damage to tea plants. Plants have developed sophisticated defense mechanisms to combat viral infections, including RNA silencing pathways that target and degrade viral nucleic acids. Resistance genes also play a crucial role in recognizing viral pathogens and initiating defense responses. The cellular and physiological features associated with these responses have been well characterized, providing insights into the mechanisms of plant resistance to viruses (Kourelis and Hoorn, 2018).

2.4 Other significant pathogens

In addition to fungi, bacteria, and viruses, other significant pathogens can affect tea plants. For instance, the fungal pathogen *Exobasidium vexans* causes blister blight, a disease that can lead to substantial crop losses. Transgenic tea plants overexpressing a class I chitinase gene from potato have shown enhanced resistance to this pathogen, demonstrating the potential of genetic engineering in improving disease resistance in tea plants (Singh et al., 2015).

3 Genetic Basis of Disease Resistance

3.1 Resistance (*R*) genes in tea plants

Resistance (*R*) genes play a crucial role in the defense mechanisms of tea plants against various pathogens. These genes encode proteins that can recognize specific pathogen-derived molecules and trigger defense responses. The majority of *R* genes encode either cell surface or intracellular receptors, which are involved in the direct or indirect perception of pathogen molecules (Figure 1) (Kourelis et al., 2018). The structural features of *R* genes, such as nucleotide-binding sites and leucine-rich repeats, are conserved across different plant species and are essential for their function (Sekhwal et al., 2015). The evolution of *R* genes is driven by mechanisms such as gene duplications, recombination, and diversifying selection, which contribute to their diversity and ability to recognize a wide range of pathogens.

The first cloned *R* gene was *Hm1* from maize, which encodes an enzyme that detoxifies HC toxin produced by the fungal pathogen *Cochliobolus carbonum*. Over the years, several models of *R* gene function have been proposed, including the guard model, the decoy model, and the NLR-ID model. *R* proteins use nine different mechanisms to

resist pathogens, which can be roughly divided into two categories: perception and loss of susceptibility. *R* genes are distributed in different host species and pathogen types, and *NLR* is the most common type of *R* gene. These identified mechanisms are not pathogen-specific, meaning that plants universally use these mechanisms to fight against various pathogens.

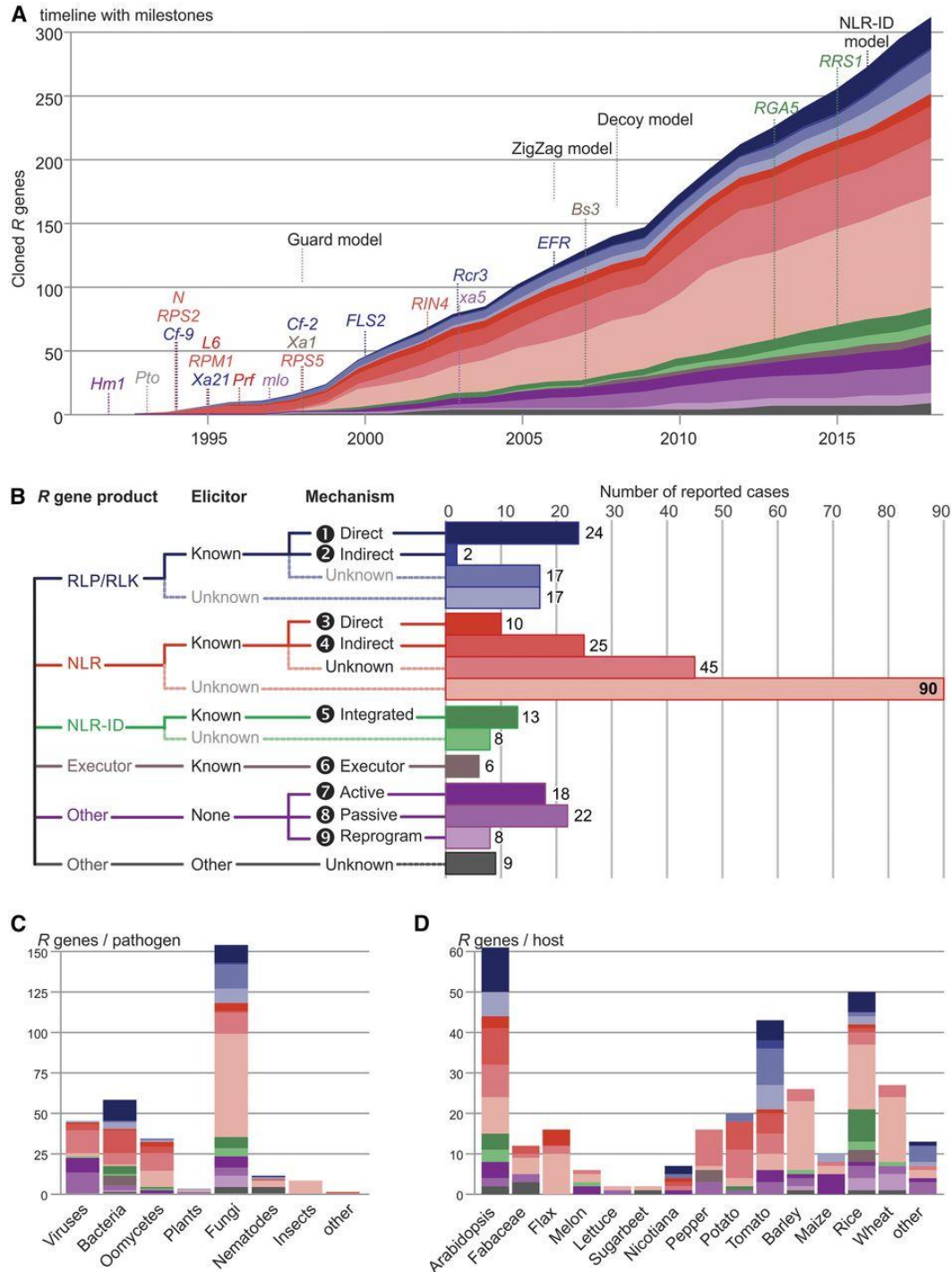


Figure 1 Analysis of molecular mechanisms underpinning *R* genes (Adopted from Kourelis et al., 2018)

Image caption: (A) A timeline summarizing the increased knowledge regarding *R* genes; (B) All identified *R* genes were grouped according to their proposed mechanism; (C) The identified *R* genes were grouped by pathogen which they act against and colored by the molecular mechanism by which they function; (D) The identified *R* genes were grouped by host species carrying them and colored by the molecular mechanism by which they function (Adopted from Kourelis et al., 2018)

3.2 Pathogen recognition mechanisms

Pathogen recognition in tea plants involves a two-tiered immune system. The first layer, known as PAMP-triggered immunity (PTI), is mediated by pattern recognition receptors (PRRs) that detect conserved microbial elicitors called pathogen-associated molecular patterns (PAMPs). The second layer, effector-triggered immunity (ETI), involves the recognition of specific pathogen effectors by intracellular R proteins, leading to a stronger and more specific defense response (Roux et al., 2014). The interaction between *R* genes and pathogen avirulence (*Avr*) genes is a key component of this recognition process, where the presence of both genes triggers a defense response. The molecular signals involved in pathogen recognition and the subsequent activation of defense mechanisms are crucial for the effective resistance of tea plants to pathogens (Zhang et al., 2013).

3.3 Genetic mapping and QTL analysis

Genetic mapping and quantitative trait locus (QTL) analysis are essential tools for identifying the genetic basis of disease resistance in tea plants. QTL analysis helps in locating regions of the genome that are associated with resistance traits, which can be influenced by multiple genes with minor effects (Zhang et al., 2013; Roux et al., 2014). The genetic background of the plant can significantly impact the expression and durability of resistance traits, as epistatic interactions between resistance genes can alter the overall resistance phenotype. High-density genome-wide genetic maps, including resistance gene analogs (RGAs), are useful for identifying QTLs and designing diagnostic markers for plant disease resistance (Sekhwal et al., 2015). These tools enable breeders to develop tea plant varieties with enhanced resistance to major pathogens by incorporating multiple resistance genes and QTLs into the breeding programs (Gallois et al., 2018).

By understanding the genetic basis of disease resistance, pathogen recognition mechanisms, and utilizing genetic mapping and QTL analysis, researchers can develop effective strategies to enhance the resistance of tea plants to major pathogens. This integrated approach will contribute to sustainable tea production and reduce the economic impact of plant diseases.

4 Signaling Pathways in Tea Plant Immunity

4.1 Salicylic acid pathway

Salicylic acid (SA) is a crucial phytohormone involved in the regulation of plant immune responses. It plays a significant role in the activation of systemic acquired resistance (SAR), a defense mechanism that provides long-lasting protection against a broad spectrum of pathogens. The SA pathway is essential for the defense against biotrophic pathogens, which feed on living host tissue. SA-mediated signaling involves the accumulation of pathogenesis-related (PR) proteins and the activation of various defense genes (An and Mou, 2011). Additionally, SA interacts with other hormones such as jasmonic acid (JA) and ethylene (ET) to fine-tune the immune response.

4.2 Jasmonic acid and ethylene pathways

Jasmonic acid (JA) and ethylene (ET) are key players in plant defense against necrotrophic pathogens, which kill host tissue and feed on the dead matter. These hormones often work synergistically to activate defense responses. The JA pathway is particularly important for induced systemic resistance (ISR), which is triggered by beneficial microbes and provides protection against a wide range of pathogens (Yang et al., 2021; Yu et al., 2022). The transcription factor ORA59 is a critical regulator in the JA/ET signaling pathway, modulating the expression of defense genes in response to pathogen attack. Furthermore, JA signaling is involved in the production of secondary metabolites that contribute to plant defense (Lin et al., 2022).

4.3 Cross-talk between signaling pathways

The interaction between SA, JA, and ET pathways, known as hormonal crosstalk, is a complex network that allows plants to fine-tune their immune responses based on the type of pathogen encountered. Crosstalk can be either synergistic or antagonistic. For instance, while SA and JA pathways often exhibit antagonistic interactions, leading to the suppression of JA-mediated defenses by SA, there are scenarios where simultaneous activation of both pathways can enhance resistance (Yang et al., 2015; Hou and Tsuda, 2022). This intricate balance is crucial

for optimizing defense responses and avoiding unnecessary energy expenditure. Additionally, other hormones such as abscisic acid, auxin, and cytokinins also interact with SA, JA, and ET pathways, further adding layers of regulation to the plant immune system (An and Mou, 2011; Sanchez et al., 2012; Yang et al., 2015).

5 Role of Secondary Metabolites

5.1 Phytoalexins and phenolics

Phytoalexins and phenolic compounds are critical in the tea plant's defense against pathogens. Phenolic acids and lignin, for instance, are synthesized in response to biotic and abiotic stresses, enhancing the plant's resistance. The *CsHCT* genes, which regulate the phenylpropanoid and lignin pathways, have been shown to increase the content of phenolic acids and lignin, thereby improving resistance to bacterial infections and abiotic stresses (Chen et al., 2021). Additionally, phenolic acids and flavonoids were found to be major metabolites in wild tea plant resources resistant to tea gray blight disease, indicating their significant role in pathogen resistance (Zhang et al., 2022). Furthermore, the synthesis of anthocyanin-3-O-galactosides, a type of phytoalexin, is induced by anthracnose infection, contributing to the hypersensitive response and resistance in tea plants (Li et al., 2023).

5.2 Flavonoids and tannins

Flavonoids and tannins are another group of secondary metabolites that contribute to the defense mechanisms of tea plants. Flavonoids, such as quercetin and kaempferol, are involved in the plant's response to pathogen infection. Overexpression of transcription factors like PalbHLH1 and PalMYB90 in poplar has been shown to increase flavonoid content and enhance resistance to fungal infections, suggesting a similar mechanism may be present in tea plants (Figure 2) (Bai et al., 2020).

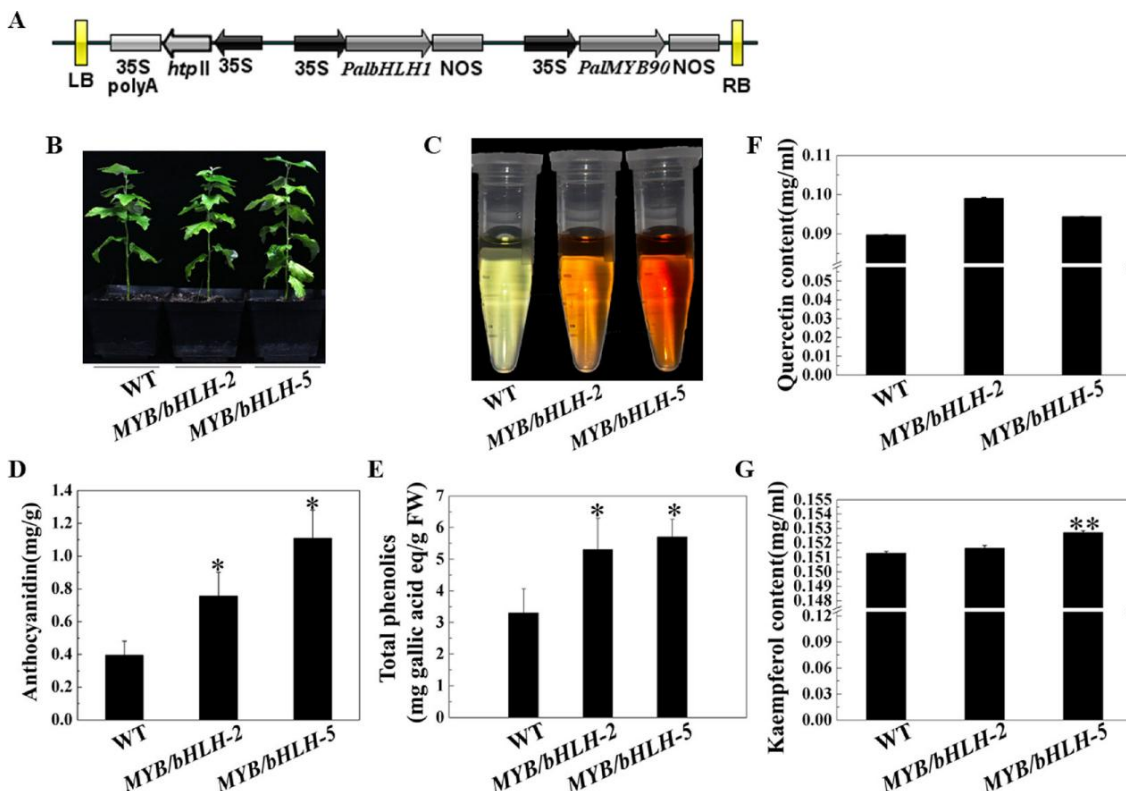


Figure 2 Characterization of transgenic poplar plants (Adopted from Bai et al., 2020)

Image caption: (A) Construction of the *MYB90/bHLH1*-OE plasmid; (B) Growth of transgenic (*MYB90/bHLH1*-OE) and wild-type (WT) poplar plants; (C) Color of anthocyanin extraction. (D) Accumulation of total anthocyanins in the leaves of *MYB90/bHLH1*-OE and WT plants. (E) Accumulation of total phenolics in the leaves of *MYB90/bHLH1*-OE and WT plants; (F, G) Contents of quercetin and kaempferol in the leaves of *MYB90/bHLH1*-OE and WT poplar plants, respectively (Adopted from Bai et al., 2020)

Overexpressing the transcription factors PalbHLH1 and PalMYB90 in poplar trees significantly enhances the plants' disease resistance, primarily by increasing the content of flavonoid compounds. These compounds include total phenols, proanthocyanidins (PAs), anthocyanins, and the intermediate products quercetin and kaempferol. Transgenic poplars exhibit enhanced antioxidant enzyme activity and hydrogen peroxide release when facing infections from *Botrytis cinerea* and *Dothiorella gregaria*, changes that are associated with the upregulation of key genes in the flavonoid metabolic pathway. Specifically, transcriptomic analysis shows that, following pathogen infection, genes related to the flavonoid biosynthesis pathway, such as PalF3H, PalDFR, PalANS, and PalANR, are significantly upregulated in poplars overexpressing PalbHLH1 and PalMYB90. These genes play critical roles in the initial, intermediate, and final steps of anthocyanin and proanthocyanidin synthesis. These findings suggest that flavonoid compounds play an important role in plant defense mechanisms, and a similar mechanism may exist in tea trees.

Additionally, the metabolic pathways for flavonoid biosynthesis are enriched in resistant tea plant resources, further supporting their role in pathogen defense (Zhang et al., 2022). Tannins, which are a type of phenolic compound, also contribute to the structural defense by reinforcing cell walls and inhibiting pathogen growth (Wink et al., 2012).

5.3 Metabolic engineering for enhanced resistance

Metabolic engineering offers a promising approach to enhance the resistance of tea plants by manipulating the biosynthetic pathways of secondary metabolites. For instance, the overexpression of *CsHCT* genes can be used to increase the production of phenolic acids and lignin, thereby improving resistance to both biotic and abiotic stresses (Chen et al., 2021). Similarly, engineering the flavonoid biosynthesis pathway by overexpressing key transcription factors can enhance the accumulation of flavonoids and improve pathogen resistance (Bai et al., 2020). Additionally, understanding the role of specific metabolites, such as anthocyanin-3-O-galactosides, in disease resistance can guide the development of resistant tea plant varieties through targeted metabolic engineering (Li et al., 2023).

6 Molecular Interactions Between Tea Plants and Pathogens

6.1 Pathogen effectors and host targets

Pathogen effectors are molecules secreted by pathogens that manipulate host cell structure and function to facilitate infection and suppress host defense mechanisms. In tea plants, these effectors are recognized by specific resistance (*R*) genes, which encode proteins that detect the presence of pathogen-derived molecules. The interaction between pathogen effectors and host targets is a critical aspect of the plant's immune response. The meta-analysis by Kourelis and Hoorn (2018) identifies nine distinct mechanisms by which *R* proteins can trigger disease resistance, including both direct and indirect perception of pathogen molecules.

6.2 Host defense responses

Upon recognition of pathogen effectors, tea plants activate a series of defense responses to combat the infection. These responses include the production of antimicrobial compounds, the strengthening of cell walls, and the activation of signaling pathways that lead to systemic acquired resistance (SAR). The transcriptome analysis by Jayaswall et al. (2016) reveals that tea plants express a variety of defense-related genes, including those encoding for defense enzymes, resistance genes, and transcription factors, in response to blister blight disease. Furthermore, the review by Zhang et al. (2013) discusses the two-tiered immune system in plants, comprising pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) and effector-triggered immunity (ETI), which collectively enhance the plant's ability to resist pathogen invasion.

6.3 Molecular arms race

The interaction between tea plants and pathogens is characterized by a continuous molecular arms race, where both the host and the pathogen evolve new strategies to outcompete each other. Pathogens evolve new effectors to overcome plant defenses, while plants, in turn, develop new *R* genes to recognize these effectors. This

co-evolutionary process is evident in the study by Cui et al. (2015), which describes how plants and pathogens are engaged in a dynamic battle, with each side constantly adapting to the other's strategies. Additionally, the rapid evolutionary rates of defense genes and their regulators in plants, driven by the need to keep pace with evolving pathogen threats.

7 Advances in Genomic and Biotechnological Approaches

7.1 Genomic sequencing and functional genomics

Genomic sequencing and functional genomics have significantly advanced our understanding of the molecular mechanisms underlying tea plant resistance to major pathogens. The advent of high-throughput sequencing technologies has enabled the identification of numerous resistance (*R*) genes and susceptibility (*S*) genes, which play crucial roles in plant-pathogen interactions. These technologies have facilitated the discovery of quantitative trait loci (QTLs) associated with disease resistance, providing valuable insights into the genetic basis of resistance (Kushalappa et al., 2016). Additionally, metabolomics and other OMICs tools have elucidated the complex biochemical pathways involved in the plant's defense mechanisms, highlighting the importance of resistance-related (RR) proteins and metabolites in reinforcing cell walls and inhibiting pathogen spread.

7.2 CRISPR and gene editing techniques

CRISPR/Cas9 and other genome editing techniques have revolutionized the field of plant disease resistance by enabling precise and targeted modifications of plant genomes. CRISPR/Cas9, in particular, has become the preferred tool due to its efficiency, simplicity, and low risk of off-target effects (Borrelli et al., 2018; Mushtaq et al., 2019). This technology has been successfully used to knock out or modify *S* genes, thereby enhancing resistance to a wide range of pathogens, including viruses, bacteria, and fungi (Langner et al., 2018; Zaynab et al., 2020). The ability to create transgene-free, disease-resistant crop varieties using CRISPR/Cas9 has significant implications for sustainable agriculture and food security (Zaidi et al., 2018; Ahmad et al., 2020). Moreover, the continuous evolution of CRISPR/Cas9 variants aims to address challenges such as off-target effects, further improving the precision and effectiveness of this technology (Das et al., 2019).

7.3 Transgenic approaches for disease resistance

Transgenic approaches have also been employed to enhance disease resistance in tea plants. By introducing specific *R* genes or antimicrobial peptides into the plant genome, researchers have developed transgenic plants with improved resistance to various pathogens. These transgenic plants often exhibit broad-spectrum resistance, making them valuable assets in the fight against plant diseases. Additionally, the integration of CRISPR/Cas9 technology with transgenic approaches has opened new avenues for developing crops with enhanced resistance. For instance, CRISPR/Cas9 can be used to precisely insert or replace genes in the plant genome, thereby creating cisgenic plants that retain the benefits of traditional breeding while incorporating advanced genetic modifications (Kushalappa et al., 2016; Borrelli et al., 2018; Zaynab et al., 2020).

8 Concluding Remarks

The molecular mechanisms of tea plant resistance to major pathogens have been extensively studied, revealing a complex interplay of genetic, biochemical, and microbial factors. Transcriptome analyses have identified numerous defense-related genes and pathways involved in resistance to blister blight, anthracnose, and tea gray blight diseases. For instance, key defense-related transcripts such as RPM1, RPS2, and RPP13 have been implicated in the salicylic acid and jasmonic acid pathways, which are crucial for overcoming the virulence of *Exobasidium vexans*. Similarly, the resistance mechanisms against *Colletotrichum* spp. involve the activation of defense signaling pathways and the development of resistant cultivars. Metabolomic and microbiome studies have highlighted the role of phenolic acids, flavonoids, and specific microbial genera in enhancing resistance to *Pestalotiopsis theae*. Additionally, strategic transcriptomic comparisons have provided insights into the molecular responses to *Ectropis oblique*, identifying key genes and pathways involved in jasmonate/ethylene signaling and terpenoid synthesis.

Continued research in this field is vital for several reasons. First, understanding the molecular basis of tea plant resistance can lead to the development of more resistant cultivars, thereby reducing crop losses and improving yield and quality. This is particularly important given the economic significance of tea as a global commodity. Second, the insights gained from these studies can be applied to other crops, enhancing our overall understanding of plant-pathogen interactions and resistance mechanisms. Third, the development of eco-friendly biocontrol strategies, as opposed to reliance on chemical fungicides, is crucial for sustainable agriculture and environmental health. Finally, the ongoing identification and characterization of resistance genes and pathways can facilitate the rational engineering of plants with enhanced resistance to a broad spectrum of pathogens.

Future studies should focus on several key areas to further advance our understanding and application of tea plant resistance mechanisms. While many resistance-related genes have been identified, their specific roles and mechanisms need to be validated through functional studies, such as gene knockout or overexpression experiments. Combining transcriptomics, metabolomics, and microbiome analyses can provide a more comprehensive understanding of the resistance mechanisms and identify potential biomarkers for resistance. Breeding programs should incorporate the identified resistance genes and pathways to develop new tea cultivars with enhanced resistance to multiple pathogens. Research should continue to explore and optimize the use of plant growth-promoting rhizobacteria and other biocontrol agents to induce systemic resistance in tea plants. Conducting long-term field studies to assess the effectiveness and stability of resistance traits under natural conditions will be crucial for practical applications. By addressing these areas, future research can significantly contribute to the sustainable cultivation of tea and other crops, ensuring food security and environmental sustainability.

Acknowledgments

Thanks very much for the feedback from the reviewers on the manuscript.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Ahmad S., Wei X., Sheng Z., Hu P., and Tang S., 2020, CRISPR/Cas9 for development of disease resistance in plants: recent progress, limitations and future prospects, *Briefings in Functional Genomics*, 19(1): 26-39.
<https://doi.org/10.1093/bfpg/elz041>
- An C., and Mou Z., 2011, Salicylic acid and its function in plant immunity, *Journal of Integrative Plant Biology*, 53(6): 412-428.
<https://doi.org/10.1111/j.1744-7909.2011.01043.x>
- Bai Q., Duan B., Ma J., Fen Y., Sun S., Long Q., Lü J., and Wan D., 2020, Coexpression of *PalbHHLH1* and *PalMYB90* genes from populus alba enhances pathogen resistance in poplar by increasing the flavonoid content, *Frontiers in Plant Science*, 10: 1772.
<https://doi.org/10.3389/fpls.2019.01772>
- Borrelli V., Brambilla V., Rogowsky P., Marocco A., and Lanubile A., 2018, The enhancement of plant disease resistance using CRISPR/Cas9 Technology, *Frontiers in Plant Science*, 9: 1245.
<https://doi.org/10.3389/fpls.2018.01245>
- Chen Y., Yi N., Yao S., Zhuang J., Fu Z., Ma J., Yin S., Jiang X., Liu Y., Gao L., and Xia T., 2021, CshCT-mediated lignin synthesis pathway involves in the response of tea plants to biotic and abiotic stresses, *Journal of Agricultural and Food Chemistry*, 69(35): 10069-10081.
<https://doi.org/10.1021/acs.jafc.1c02771>
- Cui H., Tsuda K., and Parker J., 2015, Effector-triggered immunity: from pathogen perception to robust defense, *Annual Review of Plant Biology*, 66: 487-511.
<https://doi.org/10.1146/annurev-arplant-050213-040012>
- Das A., Sharma N., and Prasad M., 2019, CRISPR/Cas9: a novel weapon in the arsenal to combat plant diseases, *Frontiers in Plant Science*, 9: 2008.
<https://doi.org/10.3389/fpls.2018.02008>
- Gallois J., Moury B., and German-Retana S., 2018, Role of the genetic background in resistance to plant viruses, *International Journal of Molecular Sciences*, 19(10): 2856.
<https://doi.org/10.3390/ijms19102856>
- Hou S., and Tsuda K., 2022, Salicylic acid and jasmonic acid crosstalk in plant immunity, *Essays in Biochemistry*, 66(5): 647-656.
<https://doi.org/10.1042/EBC20210090>

- Hu Y., Zhang M., Lu M., Wu Y., Jing T., Zhao M., Zhao Y., Feng Y., Wang J., Gao T., Zhou Z., Wu B., Jiang H., Wan X., Schwab W., and Song C., 2021, Salicylic acid carboxyl glucosyltransferase UGT87E7 regulates disease resistance in *Camellia sinensis*. *Plant Physiology*, 188: 1507-1520.
<https://doi.org/10.1093/plphys/kiab569>
- Jayaswall K., Mahajan P., Singh G., Parmar R., Seth R., Raina A., Swarnkar M., Singh A., Shankar R., and Sharma R., 2016, Transcriptome analysis reveals candidate genes involved in blister blight defense in tea (*Camellia sinensis* (L.) Kuntze), *Scientific Reports*, 6(1): 30412.
<https://doi.org/10.1038/srep30412>.
- Jin S., Ren Q., Lian L., Cai X., Bian L., Luo Z., Li Z., Ye N., Wei R., He W., Liu W., and Chen Z., 2020, Comparative transcriptomic analysis of resistant and susceptible tea cultivars in response to *Empoasca onukii* (Matsuda) damage, *Planta*, 252: 1-15.
<https://doi.org/10.1007/s00425-020-03407-0>
- Kourelis J., and Hoom R., 2018, Defended to the nines: 25 years of resistance gene cloning identifies nine mechanisms for R protein function, *Plant Cell*, 30: 285-299.
<https://doi.org/10.1105/tpc.17.00579>
- Kushalappa, A., Yogendra, K., Sarkar, K., Kage, U., and Karre S., 2016, Gene discovery and genome editing to develop cisgenic crops with improved resistance against pathogen infection, *Canadian Journal of Plant Pathology*, 38: 279-295.
<https://doi.org/10.1080/07060661.2016.1199597>
- Langner T., Kamoun S., and Belhaj K., 2018, CRISPR crops: plant genome editing toward disease resistance, *Annual Review of Phytopathology*, 56: 479-512.
<https://doi.org/10.1146/annurev-phyto-080417-050158>.
- Li T., Wang S., Shi D., Fang W., Jiang T., Zhang L., Liu Y., Gao L., and Xia T., 2023, Phosphate deficiency induced by infection promotes synthesis of anthracnose-resistant anthocyanin-3-O-galactoside phytoalexins in the *Camellia sinensis* plant, *Horticulture Research*, 10(12): uhad222.
<https://doi.org/10.1093/hr/uhad222>
- Lin S., Ye M., Li X., Xing Y., Liu M., Zhang J., and Sun X., 2022, A novel inhibitor of the jasmonic acid signaling pathway represses herbivore resistance in tea plants, *Horticulture Research*, 9: uhab038.
<https://doi.org/10.1093/hr/uhab038>
- Liu N., Wang Y., Li K., Li C., Liu B., Zhao L., Zhang X., Qu F., Gao L., Xia T., and Wang P., 2023a, Transcriptional analysis of tea plants (*Camellia sinensis*) in response to salicylic acid treatment, *Journal of Agricultural and Food Chemistry*, 71(5): 2377-2389.
<https://doi.org/10.1021/acs.jafc.2c07046>
- Liu S., Zhang S., He S., Qiao X., and Runa A., 2023b, Tea plant (*Camellia sinensis*) lipid metabolism pathway modulated by tea field microbe (*Colletotrichum camelliae*) to promote disease, *Horticulture Research*, 10(4): uhad028.
<https://doi.org/10.1093/hr/uhad028>
- Mushtaq M., Sakina A., Wani S., Shikari A., Tripathi P., Zaid A., Galla A., Abdelrahman M., Sharma M., Singh A., and Salgotra R., 2019, Harnessing genome editing techniques to engineer disease resistance in plants, *Frontiers in Plant Science*, 10: 550.
<https://doi.org/10.3389/fpls.2019.00550>
- Roux F., Voisin D., Badet T., Balagué C., Barlet X., Huard-Chauveau C., Roby D., and Raffaele S., 2014, Resistance to phytopathogens e tutti quanti: placing plant quantitative disease resistance on the map, *Molecular Plant Pathology*, 15(5): 427-432.
<https://doi.org/10.1111/mp.12138>
- Sanchez L., Courteau B., Hubert J., Kauffmann S., Renault J., Clément C., Baillieu F., and Dorey S., 2012, Rhamnolipids elicit defense responses and induce disease resistance against biotrophic, hemibiotrophic, and necrotrophic pathogens that require different signaling pathways in arabidopsis and highlight a central role for salicylic acid, *Plant Physiology*, 160: 1630-1641.
<https://doi.org/10.1104/pp.112.201913>
- Sekhwil M., Li P., Lam I., Wang X., Cloutier S., and You F., 2015, Disease resistance gene analogs (RGAs) in plants, *International Journal of Molecular Sciences*, 16: 19248-19290.
<https://doi.org/10.3390/ijms160819248>
- Singh H., Deka M., and Das S., 2015, Enhanced resistance to blister blight in transgenic tea (*Camellia sinensis* [L.] O. Kuntze) by overexpression of Class I chitinase gene from potato (*Solanum tuberosum*), *Functional & Integrative Genomics*, 15: 461-480.
<https://doi.org/10.1007/s10142-015-0436-1>
- Wang D., Li C., Ma C., and Chen L., 2015, Novel insights into the molecular mechanisms underlying the resistance of *Camellia sinensis* to *Ectropis oblique* provided by strategic transcriptomic comparisons, *Scientia Horticulturae*, 192: 429-440.
<https://doi.org/10.1016/J.SCIEN.2015.06.005>
- Wang Y., Hao X., Lu Q., Wang L., Qian W., Li N., Ding C., Wang X., and Yang Y., 2018, Transcriptome analysis and histochemistry reveal that hypersensitive cell death and H₂O₂ have crucial roles in the resistance of tea plant (*Camellia sinensis* (L.) O. Kuntze) to anthracnose, *Horticulture Research*, 5.
<https://doi.org/10.1038/s41438-018-0025-2>
- Wink M., Ashour M., and El-Readi M., 2012, Secondary metabolites from plants inhibiting ABC transporters and reversing resistance of cancer cells and microbes to cytotoxic and antimicrobial agents, *Frontiers in Microbiology*, 3: 130.
<https://doi.org/10.3389/fmicb.2012.00130>

- Yang Y., Ahammed G., Wu C., Fan S., and Zhou Y., 2015, Crosstalk among jasmonate, salicylate and ethylene signaling pathways in plant disease and immune responses, *Current Protein & Peptide Science*, 16(5): 450-461.
<https://doi.org/10.2174/1389203716666150330141638>
- Yang Y., Kim Y., Kim H., Kim S., Cho K., Kim Y., Lee D., Lee M., Kim S., Hong J., Kwon S., Choi J., and Park O., 2021, The transcription factor ORA59 exhibits dual DNA binding specificity that differentially regulates ethylene- and jasmonic acid-induced genes in plant immunity, *Plant Physiology*, 187(4): 2763-2784.
<https://doi.org/10.1093/plphys/kiab437>
- Yu Y., Gui Y., Li Z., Jiang C., Guo J., and Niu D., 2022, Induced systemic resistance for improving plant immunity by beneficial microbes, *Plants*, 11(3): 386.
<https://doi.org/10.3390/plants11030386>
- Zaidi S., Zaidi S., Mukhtar M., and Mansoor S., 2018, Genome editing: targeting susceptibility genes for plant disease resistance, *Trends in Biotechnology*, 36(9): 898-906.
<https://doi.org/10.1016/j.tibtech.2018.04.005>
- Zaynab M., Sharif Y., Fatima M., Afzal M., Aslam M., Raza M., Anwar M., Raza M., Sajjad N., Yang X., and Li S., 2020, CRISPR/Cas9 to generate plant immunity against pathogen, *Microbial Pathogenesis*, 141: 103996.
<https://doi.org/10.1016/j.micpath.2020.103996>
- Zhang Y., Lubberstedt T., and Xu M., 2013, The genetic and molecular basis of plant resistance to pathogens, *Journal of Genetics and Genomics*, 40(1): 23-35.
<https://doi.org/10.1016/j.jgg.2012.11.003>
- Zhang Y., Zhang J., Yan C., Fang M., Wang L., Huang Y., and Wang F., 2022, Metabolome and microbiome signatures in the leaves of wild tea plant resources resistant to *Pestalotiopsis theae*, *Frontiers in Microbiology*, 13: 907962.
<https://doi.org/10.3389/fmicb.2022.907962>
- Zhou L., Li X., Kotta-Loizou I., Dong K., Li S., Ni D., Hong N., Wang G., and Xu W., 2021, A mycovirus modulates the endophytic and pathogenic traits of a plant associated fungus, *The ISME Journal*, 15: 1893-1906.
<https://doi.org/10.1038/s41396-021-00892-3>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.