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http://currentagriculturetrends.vitalbiotech.org/

ISSN (E): 2583 – 1933

Curr. Agri.Tren.:e- Newsletter, (2026) *5*(4), 5-10

Current Agriculture Trends:
e-Newsletter

Article ID: 607

Resistance Genes in Tomato: Origins, Mechanisms, and Applications in Crop Enhancement

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Article History
Received: 2.4.2026
Revised: 6.4.2026
Accepted: 11.4.2026

INTRODUCTION

Solanum lycopersicum L., also known as tomato, is a member of the Solanaceae family and one of the most frequently grown vegetable crops worldwide. Though tomatoes are botanically classed as fruits, they are primarily consumed as vegetables in fresh, cooked, and processed forms due to their culinary applications and nutritional benefits (Krishna *et al.*, 2022). Tomatoes are high in vitamins, minerals, antioxidants, and dietary fiber, making them beneficial to human nutrition. This has resulted in a consistent increase in worldwide demand.

However, tomato production is particularly vulnerable to a variety of abiotic and biotic stressors. Abiotic stressors such as drought, salinity, heat, cold, flooding, and nutritional deficiencies can all have a negative impact on plant development and output. Biotic stressors caused by fungi, bacteria, viruses, nematodes, and insect pests, on the other hand, can result in considerable production and quality losses. Abiotic stressors alone can cause up to 70% yield loss in tomatoes, depending on the severity, duration, and growth stage (Krishna *et al.*, 2022). Furthermore, biotic stressors cause a 20–40% annual loss in worldwide crop production, underscoring the seriousness of pathogen-related agricultural harm (Gururani *et al.*, 2012).

Conventional management strategies like chemical control and cultural treatments have been less effective due to the increasing frequency of harsh weather events and changing pathogen populations. Chemical techniques can be expensive, hazardous to the environment, and may result in pathogen-resistant strains. Consequently, breeding for genetic resistance has emerged as a crucial tactic for controlling biotic and abiotic stresses in tomato crops. Use of Resistance (R) genes for crop improvement became a perfect method as they enable plants to recognize stress signals and initiate defence mechanisms against both biotic and abiotic stresses (McDowell & Woffenden, 2003; Jatwa *et al.*, 2017). To make efficient use of these genes in tomato improvement, we need to understand their structure, mechanisms, benefits, and downsides, which are discussed below.

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R – Gene: Structure and Classification:

Resistance (R) genes are plant genes that encode proteins that recognize stress signals or pathogen-related chemicals and activate defence responses. The majority of plant resistance genes (approx. 80%) belong to the NBS-LRR class, which produce proteins with a Nucleotide-Binding Site (NBS) domain and a Leucine-Rich Repeat (LRR) domain, also known as (NBS – LRR) R – genes. These genes are essential for plant immunity and stress tolerance because they enable rapid and precise activation of defense responses (McDowell & Woffenden, 2003; Rasul *et al.*, 2019).

The NBS domain functions as a molecular switch, binding and breaking down nucleotides such as ATP or GTP, whereas the LRR domain aids in protein interactions and ligand recognition, providing pathogen detection specificity (Gururani et al., 2012). NBS – LRR genes are classified into two subclasses based on the nature of their N-terminal domains: Toll/interleukin-1 receptor NBS – LRR (TIR-NB-LRR) and coiled-coil NBS – LRR (CC-NB-LRR), which are connected to separate signaling pathways (McDowell and Woffenden, 2003).

Table 1: Major classes of resistance gene-encoding R-proteins and their domain arrangements (Source: Rasul *et al.*, 2019). NBS: Nucleotide Binding Site; LRR: Leucine Rich Repeats; TrD: Transmembrane Domain; TIR: Toll-interleukin-1 receptor; eLRR: extracellular Leucine Rich Repeats; PEST: Pro-Glu-Ser-Thr (amino acid domain); CC: Coiled Coil; NLS: Nuclear Localization Signal domain; WRKY: conserved amino acid sequence WRKYGQK

Class	Arrangement of functional domains	Examples	
		Host	R-gene
CNL	NBS – LRR – CC	Tomato	*I2, Mi-1.2*
TNL	NBS – LRR – TIR	Tobacco, *Arabidopsis*	*N gene, RPP5*
eLRR-TrD	eLRR – TrD	Tomato	*Cf-9, Cf-4, Cf-2*
eLRR-TrD-Kinase	eLRR – TrD – Kinase	Rice	*Xa21*
LRR-TrD-PEST-ECS	LRR – TrD – PEST – ECS	Tomato	*Ve1, Ve2*
eLRR-CC	eLRR – CC	*Arabidopsis*	*RPW8*
TIR-NBS-LRR-NLS-WRKY	TIR – NBS – LRR – NLS – WRKY	*Arabidopsis*	*RRS1-R*
Enzymatic R-genes	Kinase – Kinase	Tomato	*Pto*

Mechanisms of R-Gene-mediated Resistance:

R-gene-mediated resistance works through a variety of molecular processes, facilitating plants to sense stress signals and develop effective defence responses. The most well-known mechanisms are gene-for-gene interaction, the guard hypothesis, pathogen-associated molecular pattern (PAMP)-induced immunity, and resistance via enzymatic activity (Malhotra & Agrawal, 2003; Jatwa *et al.*, 2017).

(i) Gene-For-Gene Interaction: According to the Flor gene-for-gene hypothesis, resistance develops when a plant R gene specifically recognizes a pathogen's avirulence (Avr) gene product. This detection triggers a variety of defense responses, including the hypersensitive response, which causes localized cell death and inhibits pathogen dissemination (McDowell & Woffenden, 2003; Malhotra & Agrawal, 2003). Although this system is highly specialized, rapidly evolving pathogens may be able to circumvent it.

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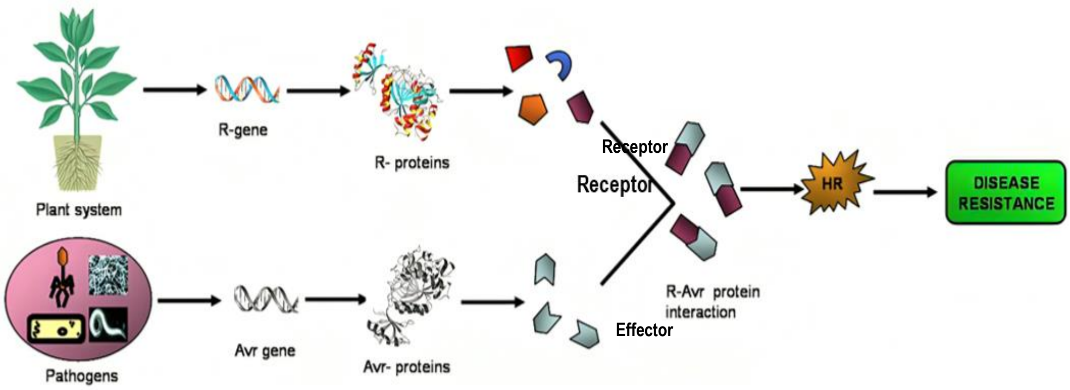

Fig 1: Plant pathogen interaction and development of disease resistance
(Source: Gururani *et al.*,2012)

Table 2: Gene-for-gene combinations and disease reaction types in a host-pathogen system in which the gene-for-gene concept operates resistance (Source: Malhotra & Agrawal, 2003)

Virulence or avirulence genes in the pathogen	Resistance or susceptibility genes in the plant	
	R(resistant) dominant	r(susceptible) recessive
A (avirulent) dominant	AR(–)	Ar(+)
a (virulent) recessive	aR(+)	ar(+)

+ = Compatible (susceptible) reaction
– = Incompatible (resistant) reaction

(ii) Guard Hypothesis: According to the guard hypothesis, resistance occurs by indirect recognition, wherein R proteins oversee ("guard") host proteins that are targeted by pathogen effectors. When an effector modifies the monitored host protein, the R protein identifies it and initiates defense signaling (McDowell & Woffenden, 2003). This method increases endurance by allowing plants to recognize many disease effectors that target the same host component.

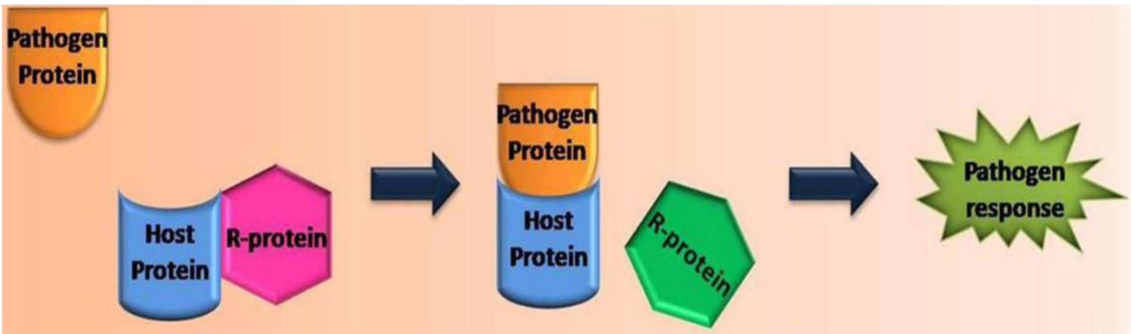

Fig 2: Guard hypothesis; the plant R proteins (guard) are associated with the endogenous host protein (guardee) which are common target proteins for the pathogens. The interaction of effector pathogen proteins with the host proteins, causes a change in their structure which is then recognized by the guard proteins. As a result, a pathogen response signaling cascade is triggered against the microbial evasion. (Source: Gururani *et al.*,2012)

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(iii) **PAMP-Triggered Immunity and Enzyme-Encoding Resistance:** Plants also have an innate immune system, which recognizes conserved pathogen-associated molecular patterns and initiates basic defense responses. Furthermore, certain resistance genes contribute to resistance by producing enzymes that fortify cell walls or detoxify pathogen metabolites (Jatwa *et al.*, 2017; Gururani *et al.*, 2012).

Role of Resistance Genes in Abiotic Stress Tolerance:

While conventional R genes are mostly associated with disease resistance, plants also use stress-responsive genes to deal with abiotic challenges. Abiotic stress tolerance is regulated by complex signaling networks that include transcription factors, hormone signaling, ion transport, and antioxidant defense systems (Zhu, 2016). These genes assist plants in recognizing stress signals and initiating adaptive reactions such as ion balance, osmotic correction, and defense against oxidative damage.

Tomato plants withstand drought stress by controlling abscisic acid signaling, transcription, and cellular water balance. Salinity responses entail ion homeostasis and detoxification, whereas heat and cold stress tolerance is dependent on protective proteins and stress-induced gene expression (Krishna *et al.*, 2022; Zhu, 2016). These stress-responsive genes function in tandem with resistance pathways to increase total plant resilience.

Applications:

- Resistance genes are frequently utilized in tomato breeding projects to generate varieties that can withstand significant biotic stressors such as fungal, bacterial, viral, and worm infections. This enhances crop stability and reduces yield losses (Jatwa *et al.*, 2017; Rasul *et al.*, 2019).
- Marker-assisted selection (MAS) frequently makes use of R genes. This technique reduces undesirable genetic features while accurately identifying and transferring resistance genes into the best tomato varieties (McDowell & Woffenden, 2003; Gururani *et al.*, 2012).
- Resistance and stress-response genes are used in genetic engineering and biotechnological techniques to increase resistance to abiotic conditions like salinity and drought. This enhances flexibility in shifting environments (Krishna *et al.*, 2022; Zhu, 2016).
- Resistance genes can also help us understand plant-pathogen interactions. They are essential for knowing the molecular mechanisms behind defensive signaling and pathogen identification (Malhotra & Agrawal, 2003; McDowell & Woffenden, 2003).
- Using resistance genes helps sustainable farming by reducing the demand for chemical pesticides and encouraging ecologically friendly disease management strategies (Gururani *et al.*, 2012).

Table 3: Different types of pathogens and their interacting Avr-genes and R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
Bacteria:				
Pseudomonas syringae pv tomato	*Lycopersicum esculentum*	Avr – Pto, Avr – PtoB	Pto	Gururani *et al.*, 2012; Rasul *et al.*, 2019
Fungi:				
Cladospoium fulvum	*Lycopersicum esculentum*	Avr2	Cf – 2	Gururani *et al.*, 2012
		Avr4	Cf – 4	
		Avr5	Cf – 5	
		Avr9	Cf – 9d	
Fusarium oxysporium	*Lycopersicum esculentum*	Avr1	I2	Gururani *et al.*, 2012
Verticillium albo -	*Solanum*	Ave1, Ave2	Ve1,Ve2	Gururani *et al.*, 2012;

atrum	*lycopersicum* (*Lycopersicum esculentum*)			Rasul *et al.*, 2019
Verticillium dahliae		Ave1	Ve1	Gururani *et al.*, 2012; Rasul *et al.*, 2019
Alternaria alternata			Asc	Rasul *et al.*, 2019
Nematode:				
Melidogyne incognita	*Lycopersicum esculentum*	-	Mi	Gururani *et al.*, 2012
Virus:				
Potato virus Y, Tobacco etch virus	*Solanum lycopersicum* spp. *Hirsutum*	Vpg	Pot – 1	Gururani *et al.*, 2012; Rasul *et al.*, 2019
Tobacco mosaic virus	*Solanum lycopersicon*	-	N gene	Gururani *et al.*, 2012
		Replicase	Tm1	
		30 kD movement protein	Tm2,Tm22	
Insect:				
Macrosiphum euphorbiae	*Lycopersicum Esculentum*	-	Mi	Gururani *et al.*, 2012

Advantages of R-Gene-Mediated Resistance:

R-gene-mediated resistance improves tomatoes in several ways. It promotes sustainable farming, lowers the need for chemical pesticides, and provides great specificity against target infections. Once introduced into elite varieties, resistance genes can give long-term protection at little additional expense (McDowell & Woffenden, 2003; Gururani *et al.*, 2012). Additionally, greater resistance can be attained by combining resistance genes through breeding techniques.

Limitations and Disadvantages:

R genes have drawbacks despite their benefits. Resistance produced by single R genes is generally race-specific and may be challenged by emerging pathogens. In breeding programs, resistance durability is a major problem (Gururani *et al.*, 2012). Furthermore, linkage drag that adversely affects agronomic qualities may result from adding resistance genes from wild relatives (McDowell & Woffenden, 2003).

Future Prospects:

Future studies should focus on identifying and characterizing novel resistance genes from a variety of genotypes, particularly tomato wild relatives. The longevity of resistance and stress tolerance can be increased by combining biotechnological and molecular breeding strategies (Krishna *et al.*, 2022; Gururani *et al.*, 2012). Developing tomato cultivars that can withstand both biotic and abiotic stress will be made easier by advances in our knowledge of stress signaling pathways and gene regulation (Zhu, 2016).

CONCLUSION

Resistance genes are critical for defending tomato crops against numerous biotic and abiotic stressors. We can effectively use them for crop development if we comprehend their structure, methods, benefits, and drawbacks. By combining resistant genes with contemporary biotechnological techniques, it is possible to create tomato cultivars that are resilient and able to sustain productivity under shifting environmental circumstances.

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