Tomato mosaic virus (ToMV) is a highly stable virus belonging to the genus Tobamovirus. It can spread through mechanical contact, contaminated tools, seeds, and workers. The disease causes mosaic patterns, mottling, and deformation of leaves, as well as fruit deformation, size reduction, and internal browning. These symptoms greatly reduce market value and processing quality, especially under greenhouse conditions (Ding et al., 2019).

Tomato hosts a very large range of viruses, with more than 300 viruses or viroids reported so far. Therefore, TYLCV and ToMV are only representative examples among many viral threats. In breeding for disease resistance, multiple viral factors need to be considered together.

3 Genetic Basis of Tomato Disease Resistance

3.1 Types of resistance

Tomato shows two main types of resistance: vertical resistance (species- or race-specific) and horizontal resistance (quantitative resistance). Vertical resistance is usually controlled by one or a few major R genes. These genes can recognize specific pathogen effectors and trigger strong defense responses. Typical examples include Ve genes for resistance to Verticillium wilt, I genes for Fusarium wilt, Mi genes for resistance to root-knot nematodes, and Ty genes for resistance to tomato yellow leaf curl disease. These genes often provide near-complete resistance, but they are easily broken by newly emerging pathogen races.

In contrast, horizontal resistance is usually controlled by multiple genes, with several QTL acting together. Each locus contributes a small effect, and this type of resistance often works against a wide range of pathogen strains. For example, resistance QTL for early blight, bacterial wilt, anthracnose, and tomato chlorosis virus (ToCV) have been widely reported (Khojasteh et al., 2024). This quantitative resistance is generally more durable, but it is relatively difficult to select and fix in breeding populations.

3.2 Resistance genes and QTL

Many key resistance genes in tomato have been cloned or mapped. The Ve locus contains Ve1 and Ve2, among which Ve1 encodes a receptor-like protein that provides resistance to race 1 of Verticillium dahliae and V. albo-atrum. The I gene family (such as I-2), located on chromosome 11, confers resistance to specific races of *Fusarium oxysporum* f. sp. lycopersici and has been widely used in commercial varieties (Orchard et al., 2023). The Mi gene provides resistance to root-knot nematodes and, in some genetic backgrounds, is also associated with resistance to other pests (Ercolano et al., 2012).

For virus resistance, several Ty genes (Ty-1 to Ty-6) derived from wild species can provide resistance or tolerance to tomato yellow leaf curl virus. Among them, Ty-2 encodes an NLR protein, and its locus has been widely used in breeding through gene pyramiding (Dhaliwal et al., 2020).

Besides major genes, meta-analysis of large-scale mapping studies has identified dozens of meta-QTL (MQTL) related to bacterial and fungal diseases. These MQTL significantly narrow down the genomic intervals and reveal candidate defense genes such as NDR1, PR proteins, and WRKY transcription factors. Individual studies have identified multiple QTL associated with resistance to early blight, bacterial wilt, anthracnose, and ToCV. These QTL usually explain moderate but significant phenotypic variation, indicating that quantitative resistance is widely present (Adhikari et al., 2023; Gebhardt, 2023).

3.3 Molecular mechanisms

At the molecular level, tomato disease resistance depends on a layered immune system. Pattern-triggered immunity (PTI) is activated when pattern recognition receptors on the cell surface detect pathogen-associated molecular patterns, leading to basic defense responses such as reactive oxygen species burst, cell wall reinforcement, and defense gene expression (Abbasi et al., 2021). Effector-triggered immunity (ETI) is mainly mediated by intracellular NLR-type R proteins, which recognize specific pathogen effectors and trigger faster and stronger responses, often accompanied by localized cell death (hypersensitive response). Genome-wide studies show that tomato contains hundreds of NLR genes, and their expression is induced during pathogen infection, highlighting their key role in ETI (Bashir et al., 2022).