Plant Archives Vol. 26, Supplement 2, 2026 pp. 3480-3491 e-ISSN:2581-6063 (online), ISSN:0972-5210

Plant Archives

Journal homepage: http://www.plantarchives.org
DOI Url : https://doi.org/10.51470/PLANTARCHIVES.2026.v26.supplement-2.442

CURRENT ADVANCES IN INHERITANCE OF TOLCNDV RESISTANCE IN CUCUMBER (*Cucumis sativus* L.): GLOBAL INSIGHTS, EVOLUTIONARY DYNAMICS, AND BREEDING STRATEGIES

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(Date of Receiving : 01-06-2026; Date of Revision : 13-07-2026; Date of Acceptance : 30-07-2026)

ABSTRACT

Tomato leaf curl New Delhi virus (ToLCNDV) has been emerging as a major limiting factor in Cucumber (*Cucumis sativus* L.) production across Asia and the Mediterranean regions, with recent reports indicating expansion into Africa and East Asia. The virus, transmitted by the whitefly *Bemisia tabaci*, can cause severe yield losses exceeding 50% under early infection and intense vector pressure. Increasing evidence highlights its rapid geographic spread and persistence in intensively cultivated systems. The evolutionary course of ToLCNDV is driven by high mutation rates, frequent recombination, and strong selection pressures, with the Indian subcontinent functioning as a major centre of its genetic diversity. Genomic studies emphasize the role of recombination in shaping host adaptation and virulence. Among available management strategies, host plant resistance remains the most sustainable approach. In Cucumber, resistance is governed by an oligogenic architecture involving major loci such as *Cy-1* and *Cy-2*, together with minor-effect quantitative trait loci, largely associated with RNA silencing–mediated antiviral defense. However, resistance efficacy is often strain-dependent. Advances in molecular markers and genomics-assisted breeding have improved the efficiency of resistance introgression, although limited cultivar availability and translational constraints remain, particularly in India. Durable resistance will require integration of gene pyramiding, standardized phenotyping protocols, and strengthened public–private partnerships. Emerging approaches, including RNA-based antivirals and genome editing, offer additional opportunities but are refrained by regulatory frameworks. This review integrates current knowledge on ToLCNDV epidemiology, evolutionary dynamics, and resistance inheritance, and proposes a framework for developing durable resistance in Cucumber under rapidly evolving viral pressure.

Keywords **:** Tomato leaf curl New Delhi virus; Cucumber (*Cucumis sativus* L.); Evolutionary dynamics; Breeding strategies

Introduction

India cultivates a wide range of Cucumber types for fresh consumption, slicing, pickling (gherkins), and processing, and the crop constitutes an important component of the country's commercial horticulture sector. Recent production statistics indicate substantial harvested area and output, with India emerging as one of the world's leading exporters of Cucumbers and gherkins, supplying a major share of the global processed gherkin market through contract farming systems concentrated in southern states (India Brand Equity Foundation [IBEF], 2022; Helgi Library, 2024; APEDA, n.d.). Globally, China dominates Cucumber and gherkin production, accounting for more than four-fifths of total world output, while most of the remaining production is concentrated in a small group of countries including Turkey, Russia, Mexico, Uzbekistan, Ukraine, Spain, and the United States. The global Cucumber and gherkin market continues to expand, with industry forecasts projecting that total market value will surpass USD 100 billion by the mid-

2030s (Index Box, 2024). Notably, production leadership does not fully align with export leadership by value; European and North American exporters such as Spain, Mexico, and the Netherlands contribute disproportionately to international trade flows (World Integrated Trade Solution [WITS], 2022).

The rising incidence of begomoviruses in cucurbit crops, extending beyond their traditional association with solanaceous hosts, reflects a notable shift in plant virus epidemiology with important implications for Cucumber production systems. Among these viruses, Tomato leaf curl New Delhi virus (ToLCNDV) has become particularly prominent, initially intensifying in India and subsequently spreading to Asia, the Mediterranean Basin, and Europe. This expansion is driven by a combination of viral adaptability, rise of protected cultivation, climate-mediated increases in vector populations, and the continuous availability of susceptible host plants. Field surveys and molecular diagnostics consistently indicate increasing disease prevalence, enhanced symptom severity, and substantial yield losses associated with ToLCNDV infection (Moriones *et al*., 2017; Karmakar *et al*., 2021; Fortes *et al*., 2022). Yield losses associated with ToLCNDV in cucurbits have been reported to vary widely, ranging from approximately 17.6% to as high as 99.4%, depending on host species, viral strain, infection timing, and environmental conditions (Patthamapornsirikul *et al*., 2025; Kadi *et al*., 2024).
Global Cucumber and gherkin production is estimated at approximately 95 million tonnes annually (FAO, 2021). Under conventional scenarios, if ToLCNDV affects 5–10% of global production areas annually with moderate disease severity (20–50% yield loss), projected losses could range from approximately 1–5 million tonnes per year (Fortes & Navas-Castillo, 2012; FAO, 2021). In India, annual Cucumber and gherkin production is approximately 1.68 million tonnes (FAO, 2021). Applying a conservative mid-range yield loss of 20–40% under moderate to severe ToLCNDV pressure, potential annual losses in affected fields could reach approximately 0.34–0.67 million tonnes, although realized losses may vary with whitefly pressure, cultivar susceptibility, and the effectiveness of integrated disease management strategies (Hanssen *et al*., 2015; Zaidi *et al*., 2020). Taken together, these estimates highlight ToLCNDV as a significant emerging constraint to Cucumber and other cucurbit production in India and globally, with severe outbreaks capable of causing 50–90% yield reductions and, in extreme cases, near-complete crop failure (Fortes & Navas-Castillo, 2012; Zaidi *et al*., 2020).

ToLCNDV is a bipartite begomovirus belonging to the family Geminiviridae and was first identified in tomato crops in India in 1995 (Padidam *et al*., 1995). For nearly two decades, the virus remained largely confined to the Indian subcontinent and parts of Asia. A major shift in its geographical distribution occurred in 2012 following its first detection in Spain, marking the onset of rapid expansion across Europe (Juárez *et al*., 2014). Subsequently, ToLCNDV has spread across Asia, Europe, the Middle East, and parts of Africa, largely driven by international movement of infected plant material and the widespread distribution of its whitefly vector, *Bemisia tabaci* (Moriones *et al*., 2017; Bragard *et al*., 2020). The virus is currently reported in 16–23 countries worldwide, depending on reporting criteria, with Asia and Europe accounting for most confirmed outbreaks (Bragard *et al*., 2020; Sáez *et al*., 2021; Koeda *et al*., 2024). The identification of genetically distinct ToLCNDV isolates in China further indicates ongoing viral diversification and continued risk of regional spread within East Asia (Gu *et al*., 2023). Field and experimental studies demonstrate that cucurbit crops infected with ToLCNDV suffer substantial growth suppression and productivity losses, frequently exceeding 20–80% in open-field systems in Mediterranean and Asian regions (Vo *et al*., 2025). Controlled inoculation studies further show that several ToLCNDV strains induce severe leaf curling, mosaic symptoms, and high viral accumulation in Cucumber, reflecting the aggressive physiological impact of the virus (Vo *et al*., 2023).

ToLCNDV has a broad host range within the Cucurbitaceae and is known to infect at least 11 cucurbit species, including Cucumber, melon, pumpkin, and squash (Sáez *et al*., 2021; Koeda *et al*., 2024). In *Cucumis sativus*, infection is characterized by pronounced leaf curling, chlorosis, growth stunting, and fruit malformation, resulting in substantial reductions in yield and marketability. In Mediterranean and Asian production systems, epidemics in susceptible Cucumber cultivars frequently exceed 50% yield loss and may approach 80% in severe epidemics, depending on cultivar susceptibility and environmental conditions (Sáez *et al*., 2021).

In India, ToLCNDV has emerged as a major threat to Cucumber and other cucurbits across both Northern and Southern regions (Table 1).

A large-scale survey conducted during 2020–2021 across Haryana, Delhi, Uttar Pradesh, Chhattisgarh, Maharashtra, Telangana, and Karnataka analyzed 551 cucurbit samples and detected begomoviruses in 124 plants, of which 47 were confirmed as ToLCNDV, indicating substantial virus prevalence across diverse

agro-ecological zones (Kumar *et al*., 2022). Typical symptoms observed in Cucumber and gourds included yellow mosaic, leaf curling, and plant stunting, consistent with ToLCNDV symptomatology reported in cucurbit hosts (Kumar *et al*., 2022; Islam *et al*., 2024). Between 2019 and 2023, a distinct ToLCNDV strain causing severe mosaic and fruit deformities was reported in Ash gourd in Udumalpet, Tamil Nadu, highlighting recent southward expansion and genetic diversification of the virus in India (Ramasamy *et al*., 2023). Collectively, ToLCNDV is now widely distributed across cucurbit production systems from Haryana and Delhi in Northern India to Telangana and Tamil Nadu in the South, with confirmed detections in Andhra Pradesh, Gujarat, Haryana, Punjab, Maharashtra, West Bengal, and Uttar Pradesh (European and Mediterranean Plant Protection Organization [EPPO], 2024; Islam *et al*., 2024). Major affected hosts include Cucumber (*Cucumis sativus*), Bottle gourd (*Lagenaria siceraria*), Bitter gourd (*Momordica charantia*), Ridge gourd (*Luffa acutangula*), Melon (*Cucumis melo*), and Pumpkin (*Cucurbita moschata*), underscoring the expanding host range and epidemiological significance of ToLCNDV in Indian cucurbit systems (EPPO, 2024; Kumar *et al*., 2022).

The economic and agronomic impacts of ToLCNDV on Cucumber cultivation are multifactorial. Yield losses result from impaired photosynthetic capacity due to leaf distortion and mosaic symptoms, as well as poor fruit set and reduced fruit quality, collectively diminishing marketable yield (Innovation Impact, 2023). In India, the rapid spread of ToLCNDV in cucurbits is strongly linked to agro-climatic conditions that favor whitefly population dynamics, complicating disease control in the absence of robust integrated pest management strategies and virus-resistant cultivars (Sujatha *et al*., 2025; Islam *et al*., 2024). Given the absence of remedial chemical treatments and the limited reliability of vector control under high whitefly pressure, host plant resistance is generally considered the most sustainable and economically viable strategy for long-term disease management in cucurbit production systems (Romay *et al*., 2019; Zaidi *et al*., 2020; Patthamapornsirikul *et al*., 2025).

The documented heterogeneity in ToLCNDV prevalence across Indian agro-ecological zones (Table 1) and the global diversity of begomovirus species infecting Cucumber and related cucurbits (Table 2) provide a critical epidemiological framework for interpreting resistance phenotypes. Resistance that is effective under localized disease pressure may not remain stable under conditions of higher viral diversity or mixed infections. Accordingly, elucidating the genetic architecture and molecular basis of ToLCNDV resistance in Cucumber requires explicit consideration of pathogen population structure, strain diversity, and mixed-infection contexts. Integrating epidemiological evidence (Tables 1 and 2) with genetic mapping, functional genomics, and breeding pipelines will facilitate the identification and pyramiding of resistance loci with broad-spectrum efficacy and durability across environments.

In this context, the present review synthesizes current advances in the inheritance and genetic architecture of ToLCNDV resistance in Cucumber, integrating global epidemiological trends, viral evolutionary dynamics, and breeding strategies. By bridging fundamental insights with applied breeding approaches, this review aims to provide a comprehensive framework for developing durable, broad-spectrum resistance and accelerating its deployment in diverse production systems, with particular emphasis on India as a centre of viral diversity and a priority region for resistance breeding.

Evolutionary Dynamics of ToLCNDV and Host Resistance

Viral Genetic Diversity, Recombination, and Geographic Structuring

The evolutionary dynamics of ToLCNDV are governed by the interaction of elevated mutation rates, recurrent recombination, and strong selection pressures imposed by host resistance and vector-mediated transmission. These processes collectively enable the continuous emergence of genetically diverse viral variants with enhanced capacity for host adaptation and increased virulence in cucurbits, including Cucumber (*Cucumis sativus* L.). Population genetic analyses from South Asia and the Mediterranean region reveal extensive intra- and inter-species recombination, particularly within genomic regions encoding the coat protein (AV1) and replication-associated protein (AC1), which are critical for host interaction and viral fitness (Padidam *et al*., 1999; García-Arenal *et al*., 2001; Lefeuvre *et al*., 2009; Fortes *et al*., 2016).

The expansion of ToLCNDV into Europe is associated with the emergence of genetically distinct Mediterranean lineages exhibiting increased fitness in zucchini, melon, and Cucumber, consistent with founder effects and directional selection following host shifts (Ruiz *et al*., 2017; Moriones *et al*., 2017). The observed geographic structuring of viral populations suggests restricted yet biologically meaningful gene

flow among regions, shaped by vector dispersal and trade-mediated movement of infected plant material.

In Cucumber, resistance is largely quantitative and oligogenic, creating heterogeneous selection pressures that can favor the emergence of resistance-weakening viral variants under sustained high inoculum pressure and monoculture-driven selection regimes (Islam *et al*., 2010; Tiwari *et al*., 2018). Comparable adaptive responses have been documented in other cucurbits, where ToLCNDV populations undergo sequence diversification and recombination in response to resistant host genotypes, reflecting reciprocal host–virus adaptation (Sáez *et al*., 2016; López *et al*., 2018). Collectively, available evidence indicates that ToLCNDV evolution occurs within a spatially structured yet interconnected network influenced by viral genetic plasticity, vector population dynamics, and host selection pressures. This framework underscores the necessity of incorporating evolutionary principles into resistance breeding, particularly through the pyramiding of complementary resistance loci to enhance durability under diverse epidemiological conditions.

Genetic Architecture and Molecular Basis of Host Resistance in Cucurbits

Resistance to ToLCNDV in Cucumber is underpinned by a multilayered genetic architecture involving major-effect loci, minor quantitative trait loci (QTLs), and background polygenic effects that collectively modulate viral replication, movement, and systemic infection. Unlike the monogenic resistance commonly reported in solanaceous crops, Cucumber exhibits predominantly quantitative resistance characterized by partial dominance and additive genetic effects, reflecting the coordinated action of multiple loci at different stages of the infection process (Islam *et al*., 2010; Tiwari *et al*., 2018). QTL mapping and genome-wide association studies have linked resistance-associated genomic regions to pathways involved in basal immunity, callose deposition, and RNA silencing competence (Wang *et al*., 2018; Li *et al*., 2021).

At the molecular level, restriction of ToLCNDV infection is closely associated with the efficiency of RNA silencing pathways and the regulation of host factors required for viral replication. Enhanced expression of key components of the RNA interference machinery, including Dicer-like (DCL), Argonaute (AGO), and RNA-dependent RNA polymerase (RDR) genes, correlates with reduced viral accumulation in tolerant genotypes (Csorba *et al*., 2015; Wang *et al*., 2019). In parallel, components of pattern-triggered immunity, including receptor-like kinases and MAP kinase cascades, contribute to early restriction of infection in epidermal and mesophyll tissues (Niehl and Heinlein, 2011; Macho and Zipfel, 2014). Phytohormone signaling networks, particularly salicylic acid and jasmonate pathways, further modulate resistance phenotypes by balancing defense activation with fitness costs under high virus pressure (Alazem and Lin, 2015).

Comparative analyses across cucurbits reinforce the conserved yet polygenic nature of ToLCNDV resistance. In melon and zucchini, resistance loci derived from wild or landrace germplasm primarily delay viral replication and restrict systemic movement rather than conferring g complete immunity (Sáez *et al*., 2016; López *et al*., 2018). Polygenic resistance has also been reported in melon and watermelon, with multiple loci contributing to reduced viral accumulation and symptom severity (Manzano *et al*., 2019; Fortes *et al*., 2022). Transcriptomic studies highlight the involvement of genes associated with cell wall reinforcement, protein turnover, and antiviral defense networks (González *et al*., 2020; Karuppusamy *et al*., 2021).

In Cucumber, a major QTL (Cy-1) has been fine-mapped to CsRDR3, a DFDGD-class RNA-dependent RNA polymerase gene linked to enhanced antiviral RNA silencing and reduced viral accumulation (Romero-Medina *et al*., 2021; Kadi *et al*., 2024). Several accessions (e.g., CGN23089, CGN23423, CGN23633) consistently show reduced symptoms and low virus titers (Romero-Medina *et al*., 2021; Kadi *et al*., 2024). Across cucurbits, resistance loci converge functionally on reinforcing RNA silencing and restricting viral replication and movement (Valli *et al*., 2023). However, the high recombination potential of ToLCNDV enables partial erosion of resistance, emphasizing the importance of pyramiding multiple QTLs and deploying genomic-assisted breeding to increase the evolutionary barrier to resistance breakdown (Mansoor *et al*., 2024).

Co-evolutionary Arms Race and Resistance Evolution in India

Host defense against ToLCNDV is mediated by multifaceted molecular mechanisms that constrain viral replication and systemic movement, with RNA-dependent RNA polymerases playing a central role in amplifying antiviral RNA silencing responses (Donaire *et al*., 2022; Valli *et al*., 2023). Resistance is predominantly quantitative, reducing viral load and symptom severity rather than offering complete immunity, and is governed by dominant, recessive, or

additive effects depending on host genetic background (Perpiñá *et al*., 2020; Paris *et al*., 2021; Zhao *et al*., 2022; Singh *et al*., 2023). In turn, ToLCNDV populations adapt through mutation and recombination, while vector population structure further shapes viral diversity and epidemic dynamics (De Barro *et al*., 2018; Fiallo-Olivé & Navas-Castillo, 2022; Mansoor *et al*., 2024).

India represents a major epicenter for ToLCNDV epidemiology and resistance evolution, with widespread virus prevalence across agroecological zones and frequent mixed infections with other begomoviruses, intensifying selection on host resistance mechanisms (Kumar *et al*., 2022; Chakraborty & Ghosh, 2023). Sustained virus pressure has generated substantial standing genetic variation in cucurbit germplasm, particularly in melon and semi-domesticated accessions, which are increasingly used as pre-breeding resources (Dhillon *et al*., 2023; Pandey *et al*., 2024). Recent advances in QTL mapping and genome-wide marker development have facilitated marker-assisted introgression of ToLCNDV resistance into elite Indian breeding lines (Rai *et al*., 2022; Singh *et al*., 2024).

These reciprocal evolutionary processes illustrate a coevolutionary arms race in which ongoing viral diversification constantly challenges host resistance. Consequently, durable management of ToLCNDV in Indian cucurbit production systems will require integrated breeding pipelines combining resistance pyramiding, genomic-assisted selection, and continuous viral surveillance to anticipate and mitigate resistance erosion (Chakraborty & Ghosh, 2023; Pandey *et al*., 2024).

Genetic Architecture, Molecular Mechanisms, Breeding Translation, and Deployment in Cucumber and Related Cucurbits

Tomato leaf curl New Delhi virus (ToLCNDV) has emerged as a major and rapidly spreading viral threat to Cucumber (*Cucumis sativus* L.) production across South and South East Asia and the Mediterranean Basin. The geographic expansion of ToLCNDV is closely linked to the global dispersal and adaptive nature of the whitefly vector *Bemisia tabaci*, intensive monoculture of cucurbits, and the absence of curative antiviral chemistries, collectively creating sustained high inoculum pressure in major production systems (Chakraborty & Ghosh, 2023; Patthamapornsirikul *et al*., 2025). The pronounced genetic plasticity of ToLCNDV driven by frequent recombination, mixed infections, and interactions with satellite molecules has facilitated rapid viral adaptation to novel hosts and resistance sources, underscoring the necessity of resistance strategies that explicitly account for viral evolutionary dynamics (Chakraborty & Ghosh, 2023; Fiallo-Olivé & Navas-Castillo, 2024). In this context, host plant resistance has emerged as the most sustainable and environmentally compatible long-term control strategy, and recent advances in germplasm discovery, genetic dissection, and genomics-enabled breeding provide an unprecedented opportunity to develop durable resistance in Cucumber and related cucurbits.

Germplasm Screening, Genetic Architecture, and Resistance Loci Discovery

Systematic Screening and Identification of Resistant Sources

Large-scale phenotypic screening of Cucumber germplasm collections using mechanical inoculation and agro-infectious partial tandem repeat clones has demonstrated that ToLCNDV resistance is rare within the cultivated gene pool. The majority of cultivated and landrace accessions exhibit high susceptibility characterized by rapid symptom development and high viral titers, reflecting the narrow genetic base of Cucumber for antiviral defense (Sáez *et al*., 2021; Islam *et al*., 2024). Notably, three Indian-origin accessions CGN23089, CGN23423, and CGN23633 consistently remain asymptomatic and accumulate extremely low levels of viral DNA across experimental systems, field validation, and generational selfing, indicating stable and heritable resistance (Sáez *et al*., 2021; Perpiñá *et al*., 2022; Saadaoui *et al*., 2023). The absence of confirmed ToLCNDV resistance in wild *Cucumis* species further highlights the constrained resistance reservoir available for Cucumber improvement and emphasizes the importance of conserving and characterizing landrace-derived diversity.

Parallel screening efforts across cucurbit crops has identified broader resistance diversity in Melon, Pumpkin, Zucchini, Sponge Gourd, Bitter Gourd, and Bottle Gourd, with several accessions displaying near-complete field resistance or strong quantitative tolerance (Dhillon *et al*., 2023; González-Ibeas *et al*., 2024). These findings not only expand pre-breeding resources but also provide a comparative background to identify conserved resistance mechanisms that may be transferable across cucurbit species through comparative genomics and candidate gene approaches.

Classical Genetic Analysis and Mapping of Resistance Loci

Genetic dissection of ToLCNDV resistance in Cucumber reveals that inheritance patterns are source-

dependent and locus-specific. In the resistant accession CGN23089, resistance is largely recessive: F_1 progeny from crosses with the susceptible cultivar BGV011742 are uniformly susceptible, while F_2 populations segregate in a ratio consistent with single-locus recessive control, although minor-effect modifiers contribute to phenotypic variance (Sáez *et al*., 2021). SNP genotyping and QTL analysis mapped a major-effect locus on chromosome 2 accounting for ~15–17% of symptom variance, with additional minor QTLs contributing to quantitative resistance components.

Subsequent mapping in the Japanese accession "No.44" revealed a distinct genetic framework comprising a dominant major locus, Cy-1, on chromosome 1 and a weaker-effect locus on chromosome 2 (Koeda *et al*., 2024). Fine-mapping delimited Cy-1 to a 209 kb region harbouring CsRDR3, whereas independent QTL-seq analysis in DC91 × DC773 populations identified a third major resistance locus, Cy-2, on chromosome 7, flanked by SSR, InDel, and CAPS markers (Ghoshal *et al*., 2025). Collectively, these studies demonstrate that ToLCNDV resistance in Cucumber is oligogenic, involving at least three major loci with contrasting dominance relationships (Cy-1, dominant; Chr. 2 QTL, recessive; Cy-2, major-effect QTL) and additional minor-effect modifiers that shape quantitative resistance expression. This architecture has direct implications for breeding strategy, particularly for pyramiding complementary loci to enhance durability and breadth of resistance.

Molecular and Mechanistic Basis of Resistance and Host–Virus Coevolution

CsRDR3 and RNA Silencing as Central Antiviral Mechanisms

Functional dissection of Cy-1 established CsRDR3, a DFDGD-class RNA-dependent RNA polymerase, as a causal resistance gene in Cucumber (Koeda *et al*., 2024). Resistant alleles of CsRDR3 harbour multiple amino acid substitutions and promoter deletions that confer elevated inducible expression following ToLCNDV infection. Virus-induced gene silencing of CsRDR3 abolishes resistance in otherwise resistant genotypes, providing direct mechanistic evidence that enhanced amplification of virus-derived small interfering RNAs (vsiRNAs) is central to restricting viral replication and systemic movement. Resistant Cucumber accessions, including CGN23089 and No.44, exhibit sharply reduced viral DNA accumulation and attenuated symptom expression, linking genotype to molecular phenotype (Sáez *et al*., 2021; Koeda *et al*., 2024).

DFDGD-class RDRs are recurrent targets of resistance evolution across crop species; homologous genes underlie durable resistance to begomoviruses in tomato (Ty-1/Ty-3) and pepper (Pepy-2), indicating partial conservation of antiviral defense strategies across plant families. The convergence of resistance on RNA silencing amplification suggests that ToLCNDV-host coevolution is formed by reciprocal adaptation between viral suppressors of RNA silencing and host capacity to amplify antiviral siRNA responses, creating a molecular arms race with direct consequences for resistance durability.

Broader Defense Networks and Comparative Mechanisms across Cucurbits

Although Cucumber-specific transcriptomic and proteomic analyses during ToLCNDV infection remain limited, mechanistic insights from melon indicate that resistance is embedded within a broader defense network involving jasmonate-mediated signaling, modulation of photosynthesis-related pathways, sugar transport, and reinforcement of cell wall integrity, in addition to core RNA silencing machinery (Sáez *et al*., 2021). These pathways likely influence viral movement competence and host tolerance to infection.

Comparative genetic analyses across cucurbits further reveal diverse inheritance modes, ranging from recessive QTLs in Cucumber (Chr. 2) and pumpkin (Chr. 8) to dominant major genes in Cucumber (Cy-1) and zucchini (BSUAL-252) (Romero Masegosa *et al*., 2020; Paris *et al*., 2021; Singh *et al*., 2023). The observed synteny between resistance regions in melon chromosome 11 and pumpkin chromosome 8 suggests partially conserved resistance architectures, potentially reflecting shared evolutionary constraints imposed by begomovirus infection (Romero Masegosa *et al*., 2020; Pérez Moro *et al*., 2024). These comparative insights support the use of cross-species candidate gene mining and marker transfer to accelerate resistance discovery in Cucumber.

Breeding Translation: Marker Development, Pyramiding Strategies, and Current Status

Marker Resources and Genomics-Enabled Selection

Identification of major resistance loci has facilitated the development of molecular markers for translational breeding. SNP markers flanking the chromosome 2 resistance region (Sáez *et al*., 2021), gene-based functional markers for CsRDR3 at Cy-1 (Koeda *et al*., 2024; Wang *et al*., 2023), and CAPS/SSR markers linked to Cy-2 (Ghoshal *et al*., 2025) collectively enable early-generation selection and precise introgression of resistance alleles. Marker-assisted selection (MAS) is now being widely

integrated into cucurbit breeding programs as a precision tool for accelerating resistance introgression. The availability of tightly linked SNP, CAPS, and gene-based functional markers associated with major resistance loci enables early-generation selection and reduces dependence on phenotyping under high disease pressure. This transition toward genomics-assisted breeding has significantly improved selection efficiency and shortened breeding cycles (Bohra *et al*., 2022; Saadaoui *et al*., 2023).

Evidence from melon (*Cucumis melo*), a closely related cucurbit with polygenic resistance to ToLCNDV, demonstrates that pyramiding major and minor QTLs improves resistance stability across environments (Perpiñá *et al*., 2022; González-Ibeas *et al*., 2024). This strategy is directly relevant to Cucumber (*Cucumis sativus*), and comparably, these disparities highlight translational bottlenecks resistance architectures exist. Accordingly, the integration of QTL-linked SNP markers, functional markers, and haplotype-based selection frameworks offers a genomics-enabled pathway to enhance resistance durability in Cucumber.

Translational Bottlenecks and Deployment Status

Conventional breeding programs have initiated backcross-based introgression of resistance from CGN23089 and related donors into elite Cucumber backgrounds, supported by marker-assisted selection to track Cy-1, Cy-2, and chromosome 2 QTL alleles (Sáez *et al*., 2021). However, despite these advances, no commercially released ToLCNDV-resistant Cucumber cultivar is currently available in India, and resistance deployment remains largely confined to pre-breeding pipelines and experimental populations (Pandey *et al*., 2024). In contrast, resistant hybrids have entered commercialization in parts of Europe through private-sector breeding pipelines, demonstrating the technical feasibility of combining resistance with high yield and market-preferred fruit quality traits (Rubio *et al*., 2023). These differences highlight existing translational bottlenecks related to breeding capacity, seed system integration, and public–private coordination in regions with the highest disease burden.

Substantial progress has been made over the last decade in dissecting the genetic basis of resistance to Tomato leaf curl New Delhi virus (ToLCNDV) in Cucumber and related cucurbit species. Resistance sources have been identified from cultivated accessions, landraces, and wild germplasm, with inheritance patterns ranging from single-gene dominant or recessive control to complex polygenic architectures. Cucumber resistance is largely determined by major-effect loci supported by modifier QTLs, in contrast to melon and Cucurbita spp., where both monogenic and oligogenic systems occur. Mapping of these loci and the discovery of candidate genes underpin marker-assisted introgression and the strategic pyramiding of resistance. A comparison of resistance sources, inheritance patterns, and mapped genomic regions across cucurbit species is summarized in Tables 3 and 4.

Emerging Technologies and Prospects for Durable Resistance

Genomic approaches such as QTL-seq have proven effective for rapid locus discovery (Ghoshal *et al*., 2025), and future application of GWAS and genomic selection is anticipated as resistant diversity extensions. Precision breeding approaches offer additional routes to enhance resistance durability. CRISPR/Cas-mediated knockout of eIF4E in Cucumber confers viral resistance (Chung *et al*., 2023), suggesting that targeted editing of susceptibility factors or regulatory modification of CsRDR3 could generate non-transgenic resistant cultivars.

Complementary non-transgenic antiviral strategies are emerging, including topical application of dsRNA "viral vaccines," which reduced ToLCNDV infection in zucchini (Noris *et al*., 2024), and RNAi-based constructs targeting viral genomes, which demonstrate strong antiviral efficacy in experimental systems (Ali *et al*., 2023). Although regulatory and public acceptance constraints limit immediate field deployment in India, these technologies provide proof-of-concept tools to complement conventional resistance breeding and to buffer production systems under epidemic conditions (Zhu *et al*., 2020; Dalakouras *et al*., 2020).

Breeding Strategies and Implementation

The translation of ToLCNDV resistance from genetic discovery to cultivar release requires a coordinated breeding pipeline that integrates germplasm exploration, molecular dissection of resistance, genomics-assisted selection, and rigorous multi-environment validation. In Cucumber, resistance sources remain limited and largely confined to a few accessions of Indian and East Asian origin, while the genetic architecture of resistance is defined by a small number of major-effect loci complemented by minor quantitative trait loci. These constraints call for breeding strategies that simultaneously maximize selection efficiency, minimize linkage drag, and enhance resistance durability through pyramiding and genomic-assisted approaches.

Recent advances in QTL mapping, functional gene discovery, and marker development have substantially improved the feasibility of marker-assisted selection (MAS) for ToLCNDV resistance in Cucumber. Functional markers derived from the resistance-associated RNA-dependent RNA polymerase gene CsRDR3 enable direct tracking of causative alleles, while tightly linked SNP, CAPS, and SSR markers associated with additional resistance loci on chromosomes 2 and 7 facilitate pyramiding of complementary resistance sources. The integration of these markers into early-generation selection pipelines reduces dependency on phenotyping under high disease pressure and accelerates introgression of resistance into elite breeding backgrounds without compromising agronomic performance.

Beyond MAS, genomics-enabled approaches, including QTL-seq and high-density SNP genotyping, provide scalable platforms for rapid locus identification and selection across diverse breeding populations. Although genome-wide association studies and genomic selection have not yet been widely implemented for ToLCNDV resistance in Cucumber, their adoption is expected to enhance prediction accuracy for quantitatively inherited resistance and facilitate simultaneous improvement of resistance and yield-related traits. Emerging precision-breeding approaches, such as targeted editing of host susceptibility factors and modulation of antiviral RNA silencing components, further expand the toolkit for developing resistant cultivars, although regulatory and acceptance constraints currently limit their immediate deployment in several regions.

To ensure effective deployment of these improvements, a stepwise breeding roadmap that links discovery, selection, validation, and commercialization is essential (Table 5). This outlines the integration of phenotyping and molecular diagnostics at early stages, genomics-assisted locus discovery and marker development at intermediate stages, and multi-location field validation and seed system engagement at later stages to ensure durable adoption by growers.

The implementation of this roadmap requires sustained integration between virology, genomics, and breeding pipelines, alongside coordinated surveillance of viral population diversity to ensure that deployed resistance remains effective across evolving ToLCNDV strains. Public–private partnerships and extension linkages will be central to accelerating the movement of resistant breeding lines from pre-breeding pipelines into commercially viable hybrids, particularly in regions such as India where ToLCNDV pressure is high and resistant cultivars are not yet widely available.

Surveillance, Diagnostics, and Integrated Disease Management

Effective resistance deployment must be embedded within robust surveillance and diagnostics frameworks. In India, coordinated monitoring of begomoviruses employs species-specific PCR and rolling circle amplification for large-scale field surveys and confirmation of ToLCNDV infections (Kumar *et al*., 2022; Sivalingam *et al*., 2023). Field-deployable nucleic acid amplification methods, including LAMP and recombinase polymerase amplification, have enhanced near–real-time detection capacity in major cucurbit-growing regions (Khan *et al*., 2023). Agroinfectious partial tandem repeat clones provide standardized pathogenicity assays for resistance phenotyping (Islam *et al*., 2024), while serological tools (DAS-ELISA and lateral-flow immunostrips) support extension-level diagnostics despite lower sensitivity for early-stage infections (Sivalingam *et al*., 2023).

Given the high recombination potential and regionally structured diversity of ToLCNDV populations, resistance must be integrated with vector management and cultural practices to reduce inoculum pressure and delay resistance erosion. Current integrated pest management recommendations emphasize sanitation, use of virus-free planting material, insect-proof nursery structures, reflective mulches, biological control agents, and judicious insecticide rotation to mitigate resistance development in whitefly populations (Chakraborty & Ghosh, 2023; Fiallo-Olivé & Navas-Castillo, 2024). Routine validation of resistance sources against geographically diverse viral isolates remains crucial to anticipate resistance breakdown under evolving epidemic pressures (Patthamapornsirikul *et al*., 2025).

Regulatory, Extension, and International Collaboration

The pace and fairness of ToLCNDV resistance deployment are strongly shaped by regulatory frameworks, seed certification systems, and extension capacity. In India, current advisory frameworks prioritize integrated pest management in the absence of resistant cultivars, underscoring the need for standardized, crop- and virus-specific operational guidelines and farmer-facing decision support tools (Kumar *et al*., 2022; Chakraborty & Ghosh, 2023).

International collaborations are pivotal for strengthening national breeding pipelines. Programs coordinated by World Vegetable Center facilitate

access to begomovirus-resistant cucurbit germplasm, advanced diagnostics, and pre-breeding materials (Dhillon *et al*., 2023). Multinational consortia integrating virology, vector ecology, and breeding provide platforms for comparative evaluation of resistance sources across diverse ToLCNDV populations and agroecological contexts, enhancing the durability and transferability of resistance strategies (García-Arenal *et al*., 2023; Patthamapornsirikul *et al*., 2025).

Challenges and Future Research Priorities

The narrow resistance base in Cucumber, combined with the rapid evolutionary potential of ToLCNDV, poses a continuing risk of resistance erosion. Priority research directions include expanded germplasm screening to capture untapped resistance diversity, fine-mapping and cloning of all major and minor resistance loci (including the chromosome 2 QTL), integrative transcriptomic and proteomic analyses to elucidate host defense networks, and routine viral population genomics to anticipate resistance-breaking variants. Durable control of ToLCNDV in Cucumber will ultimately depend on coordinated integration of resistance pyramiding, genomics-enabled breeding, evolutionary surveillance, and integrated disease management within supportive regulatory and extension frameworks.

Conclusion

Long-term management of ToLCNDV in Cucumber will depend on aligning resistance breeding strategies with the evolutionary dynamics of regionally diverse viral populations. By integrating advances in resistance genetics, genomic tools, and comparative insights from related cucurbit species, this review outlines a strategic framework for developing durable and broad-spectrum resistance. In the Indian context, where viral diversity and disease pressure are particularly high, prioritizing well-characterized resistance donors, implementing marker-assisted pyramiding, and strengthening coordination between breeding programs and viral surveillance systems will be critical for accelerating the development and deployment of resistant cultivars.

Table 1 : Distribution of Tomato leaf curl New Delhi virus (ToLCNDV) in Cucumber and cucurbit crops in India

Agro-ecological Region	*States / Locations surveyed	Host(s) reported (Cucurbitaceae)	Evidence type	Key reference(s)
North India	Haryana, Delhi, Uttar Pradesh, Punjab	Cucumber, bottle gourd, ridge gourd, bitter gourd	PCR detection and sequencing of ToLCNDV isolates	Kumar *et al*., 2022; EPPO, 2024
Central India	Chhattisgarh, Madhya Pradesh	Mixed cucurbits including Cucumber	PCR-based molecular diagnosis	Kumar *et al*., 2022
West India	Maharashtra, Gujarat	Cucumber, pumpkin, bottle gourd	PCR confirmation of ToLCNDV in cucurbits	Kumar *et al*., 2022; EPPO, 2024
South India	Karnataka, Telangana, Andhra Pradesh, Tamil Nadu	Cucumber and multiple gourds; ash gourd (severe outbreaks in Tamil Nadu)	PCR detection; partial genome sequencing of ToLCNDV strains	Kumar *et al*., 2022; Ramasamy *et al*., 2023; Islam *et al*., 2024
East India	West Bengal, Odisha, Bihar (adjacent to Bangladesh)	Mixed cucurbits; Cucumber less frequently sampled	Regional surveys and molecular detection of begomoviruses including ToLCNDV	EPPO, 2024; Islam *et al*., 2024

***** Distribution records are based on peer-reviewed surveys and official plant protection reports. Absence

Table 2 : Major begomoviruses reported to infect Cucumber globally and in India

Begomovirus species	*Host (Cucumber context)	Country / Region	Evidence type	Reference (Author, Year)	Representative GenBank accession(s)*
Tomato leaf curl New Delhi virus (ToLCNDV)	Cucumber	India (eastern sub-Himalayan region)	PCR + sequencing	Karmakar *et al*., 2021	KC545812 (related isolate)
ToLCNDV	Cucumber (predominant in cucurbits)	India (north, central, south)	PCR surveys	Nayaka *et al*., 2023	Not specified
ToLCNDV	Cucumber	Algeria	Genome sequencing	Juárez *et al*., 2019	MK981891

ToLCNDV	Cucumber	Cambodia	Genome sequencing	Reports, 2020	MT682358
ToLCNDV	Cucumber	Indonesia (Java)	DNA-A & DNA-B sequencing	Mizutani *et al*., 2011	AB613825, AB613826
ToLCNDV	Cucumber (comparative reference isolate)	Thailand	Reference genome	Ito *et al*., 2008	AB330079, AB330080
Tomato leaf curl Palampur virus (ToLCPalV)	Cucumber (mixed cucurbit infections)	India (northern India)	PCR detection	Nayaka *et al*., 2023	Not available
ToLCPalV (related isolates)	Cucumber (mixed infection)	Saudi Arabia	PCR + partial sequencing	Sattar *et al*., 2024	Reported (DNA-A & DNA-B)
Watermelon chlorotic stunt virus (WmCSV)	Cucumber (incidental host)	Saudi Arabia / Middle East	PCR + genome sequencing	Sattar *et al*., 2024	JN618984 (representative)
Squash leaf curl virus (SqLCV)	Cucumber (mixed infections)	Saudi Arabia	PCR detection in mixed infections	Amer *et al*., 2025	Not specified

*Host associations represent natural field infections unless stated otherwise. Mixed begomovirus infections are common in cucurbits and may intensify disease severity. Accession numbers are representative where available.

Table 3 : Genetic sources and inheritance patterns of resistance to Tomato leaf curl New Delhi virus (ToLCNDV) in Cucumber and selected cucurbit crops

Species / Crop group	Resistance source	Genetic control	Key genomic regions / candidate genes
Cucumber (*Cucumis sativus*)	Indian accessions (CGN23089, CGN23423, CGN23633)	Recessive	Major QTL on chromosome 2
	Cucumber accession No. 44	Dominant major locus (Cy-1)	*CsRDR3* on chromosome 1
	Newly screened breeding lines (e.g., ABS.PE.045, ABS.PE.048)	Polygenic (multiple QTLs)	QTLs on chromosomes 1, 2, 6, and 7
Melon (*Cucumis melo*)	Wild Indian accessions (e.g., WM-7)	Major locus with modifier regions	Major QTL on chromosome 11; minor QTLs on chromosomes 2 and 12
Pumpkin / squash (*Cucurbita* spp.)	Zucchini accession BSUAL-252	Dominant single gene	Locus not yet mapped
	Cucurbita moschata landraces	Recessive major QTL	QTL on chromosome 8
Sponge gourd (*Luffa cylindrica*)	Indian germplasm accessions	Dominant single gene	Locus not yet mapped

Table 4 : Chromosomal localization and mode of inheritance of major ToLCNDV resistance loci in cucurbit crops

Species	Chromosomal location of resistance locus	Gene/QTL	Mode of inheritance
Cucumber (*Cucumis sativus*)	Chromosome 2	SNP-linked QTL	Recessive
Cucumber (*Cucumis sativus*)	Chromosome 1	*CsRDR3* (Cy-1 locus)	Dominant
Melon (*Cucumis melo*)	Chromosome 11	Major-effect QTL	Complex (epistatic with minor loci)
Pumpkin (*Cucurbita moschata*)	Chromosome 8	Major QTL	Recessive
Zucchini (*Cucurbita pepo*)	Not fully mapped	Novel dominant gene	Dominant
Sponge gourd (*Luffa cylindrica*)	Not fully mapped	Single dominant gene	Dominant

Table 5 : Strategic roadmap for deployment of ToLCNDV resistance in Cucumber breeding

Breeding step	Tools/Approach	Objective
Germplasm screening	Phenotyping under controlled inoculation; molecular diagnostics (PCR/RCA)	Identify stable and broad-spectrum resistance sources
Genetic mapping	QTL mapping, QTL-seq, candidate gene analysis	Localize major and minor resistance loci

Marker development	SNP markers linked to CsRDR3 and chromosome 2 QTL; functional gene-based markers	Enable marker-assisted selection (MAS)
Crossing & selection	MAS combined with genomic selection and pyramiding strategies	Develop elite resistant breeding lines
Field evaluation	Multi-location and multi-season trials under natural infection pressure	Validate resistance stability and agronomic performance
Commercial release	Seed multiplication; regulatory approval; extension linkage	Facilitate large-scale adoption by growers

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