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REVIEW ARTICLE

Unraveling the devastating impact of *Tomato Leaf Curl New Delhi Virus* (ToLCNDV): understanding its characteristics, host range, and management strategies

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ABSTRACT

Due to their stagnation, plants are frequently exposed to a variety of stresses, including both abiotic and biotic factors. Biotic stress in plants is due to many microbes that include viruses, fungi, bacteria, and parasitic organisms as plant pathogens. Plant viruses are one of those pathogens that frequently evolve and lower global agricultural productivity. Geminiviruses are the most damaging type of plant viruses. *Tomato Leaf Curl New Delhi Virus* (ToLCNDV) is a begomovirus belonging to the family Geminiviridae. This is a ssDNA virus having a bipartite genome with genomic length ranging between 2.6-2.7 kb. This virus was originally discovered in India in 1995 from tomato *(Lycopersicon esculentum)*. It mostly infects solanaceous and cucurbitaceous crops and is a whitefly-transmitted, circulative and persistent virus. Its prominent symptoms are severe upward leaf curling, enations, stunting, puckering, yellow spots and yellow mosaic. This virus has devastating effects on the yield of different crops with yield losses ranging between 17.6-99.4 % depending upon the disease-causing factors. ToLCNDV-ES and ToLCNDV-OM are the most devastating strains of this virus. This comprehensive review will provide basic information on the characteristic features of ToLCNDV. The evolutionary mechanism of this virus is studied to know about the strain's evolution with the passage of time on different host plants cultivated in several regions of the world. This review also covers the genome characteristics, geographical distribution, host range, transmission methods, genetic diversity, different molecular & serological assays, yield losses, and the management of this virus.

KEYWORDS, ToLCNDV, virus detection, host range, evolution, threat management

Introduction

Taxonomy

In tropical and subtropical regions, viruses belonging to the Geminiviridae family can infect many monocotyledonous and dicotyledonous plants and cause devastating damage. The Begomovirus is a successful group of newly emerging plant viruses (Fiallo-Olivé & Navas-Castillo, 2023). Regarding the genetic diversity and geographical origin, the genus is divided into two phylogenetic groups: New World (NW) which includes *Desmodium Leaf Distortion Virus* (DesLDV) and *Corchorus Yellow Vein Cuba Virus* (CoYVCUV) and Old World (OW) includes *Tomato yellow leaf curl Thailand virus* (TYLCTHV), *Cotton Leaf Curl Virus* (CLCuV) and *Tomato Yellow Leaf Curl Virus* (TYLCV) (Farina et al., 2023). Among the old world, ToLCNDV is a devastating begomovirus that infects solanaceous plants, such as tomato and chili crops, and was originally discovered in India in 1995 (Alfaro-Fernández et al., 2016; Bragard et al., 2020; Hussain et al., 2005; Janssen et al., 2022).

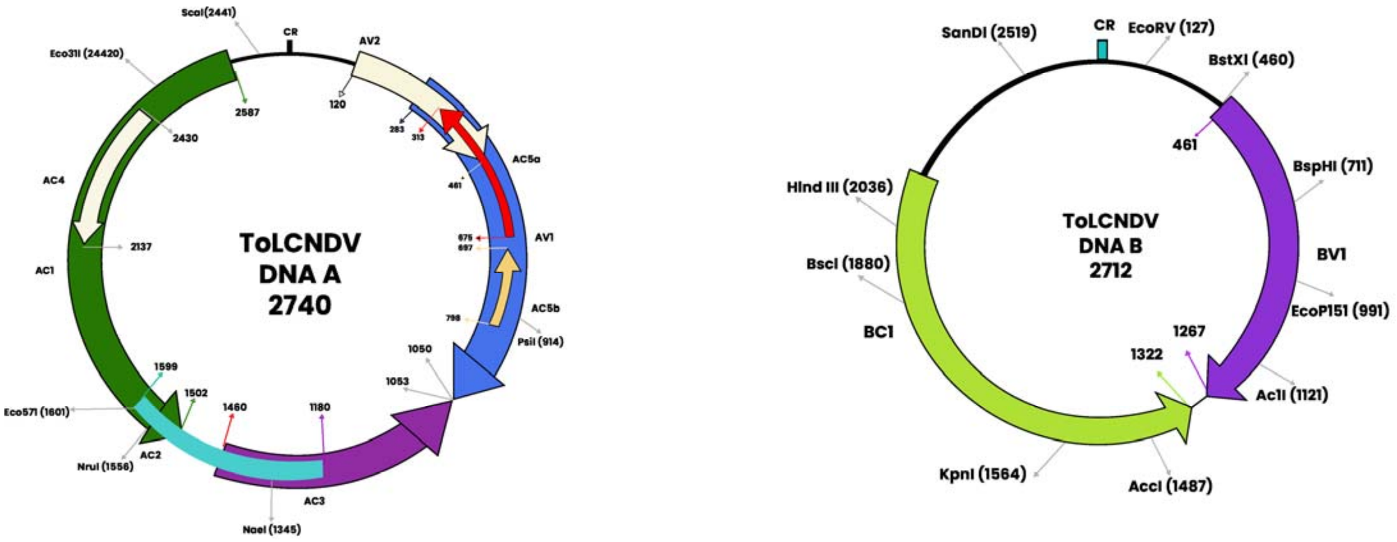

Figure 1. *Schematic representation illustrating the genomic organization of Tomato leaf curl New Delhi virus (ToLCNDV). The virus consists of two genomic components, DNA-A and DNA-B, each containing specific genes shown as arrows. DNA-A encodes essential proteins for virus replication (Rep), replication enhancement (REn), transcriptional activation (TrA), viral coat protein (CP), as well as AV2 and AC4 proteins. Meanwhile, DNA-B contains genes responsible for viral movement protein (MP) and nuclear shuttle protein (NSP).*

Genome

The genome of ToLCNDV is made up of two circular ssDNA molecules, i.e., DNA-A and DNA-B, with a genomic length varying in a range of 2.7 and 2.6 kb, respectively. DNA A codes for five different proteins including (i) coat protein (AV1/V1 and AV2/V2), which is thought to play a vital role in the movement of the virions, whereas the complementary-sense strand codes for (ii) replication-associated protein (RepA, AC1/C1), (iii) a transcriptional activator protein (AC2/C2), (iv) a replication enhancer protein (AC3/C3), and (v) C4 protein (AC4/C4). On the other hand, DNA B codes for two proteins that are (i) nuclear shuttle protein (BV1) and (ii) movement protein (BC1) (Viruses & King, 2011). DNA-A can replicate itself and codes for viral replication and encapsidation. DNA-B is involved in the synthesis of two intercellular and intracellular proteins associated with the virus movement (Rogers et al., 1986). For replication, systemic infection, movement, manifestation and nuclear localization DNA-B needs DNA-A (Sanderfoot & Lazarowitz, 1996). These genomic

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elements (DNA-A and DNA-B) possess a common region known as intergenic region (IR) that controls necessary patterns that are essential for the regulation of genetic expression and the initiation of replication. Both DNAs contain the common region (CR), that is present within the intergenic region. CR-region has a hairpin structure with a conserved nonanucleotide sequence (TAATATTAC↓) that spans the origin of the virion replication strand (ORI, denoted by ↓), which is a key topological character ↓ (Padidam et al., 1995). Each bipartite begomovirus has two components, and within the IR, there is a common region (CR) that is hardly 200 nt long.

Geographical distribution

The early record of the existence of ToLCNDV is available from India where it was reported to infect tomato (*Solanum lycopersicum* L.) crop and other horticultural crops successively, i,e: potato (*S. tuberosum* L.), zucchini squash (*Cucurbita pepo*), eggplant (*S. melongena L.*), and chilli pepper (*Capsicum annuum* L.) (Luigi et al., 2019). ToLCNDV was reported in 2004 to infect chilli pepper plants located in Punjab, Pakistan (Hussain et al., 2004). This is the only begomovirus that has no movement restrictions through the countries located in Europe and Asia. As it has been reported to infect important crops cultivated in Iran, Sri Lanka, Taiwan (China), Malaysia, Thailand, Indonesia, and Bangladesh in the Asian continent. In 2006, this virus was isolated from Chilli fields around Lucknow, Uttar Pradesh, India (Khan et al., 2006). Cucumber (*Cucumis sativus* L.) is an important vegetable for Indonesians. In August 2008, cucumber plants grown in Klaten, Central Java, Indonesia showed the symptoms like yellowing and green mosaic patterns on leaves (Mizutani et al., 2011). This virus poses a particular hazard to zucchini squash (*C. pepo*), a cucurbitaceous crop. In 2012, ToLCNDV was found for the first time in Europe, impacting tomatoes, melon, and zucchini squash, mostly in Spain (Juárez et al., 2014). Later, confirmation that the virus came from Algeria, Tunisia, Morocco, Estonia, Greece, Italy, Portugal, and Spain (Phaneendra et al., 2012). Later it was reported to be active in Pakistan, Sri Lanka, and Bangladesh (in the Indian subcontinent), in the Philippines, Indonesia, Thailand, and Chinese Taiwan (in Southeast Asia), and in Iran (Middle East) (Kil et al., 2020). In the Mediterranean basin, this virus was reported in Spain, Tunisia, Italy, Morocco, Greece, Algeria, and France (Desbiez et al., 2021; Juárez et al., 2014). In Italy, it was discovered for the first time in the province of Trapani (Sicily's) horticultural area in October 2015, where severe and typical symptoms appeared on zucchini squash plants in an open field. However, it was not reported earlier by the growers (Panno et al., 2016); after that, the disease was reported from Sardinia (Luigi et al., 2016), Lazio (Bertin et al., 2018), Calabria, Campania, and Apulia states (Trisciuzzi et al., 2018). In September 2013, symptoms of chlorotic mottling and vein distortion were observed on the lower to middle leaves of tomatoes grown at the greenhouse of the province of Almeria, Spain (Ruiz et al., 2015). In Kébili region (Southeastern Tunisia) during the year 2015, a destructive disease affecting many plants, generally sustaining in the crops until the end of the season, was observed on cucurbits (melon, cucumber and zucchini) grown under plastic tunnels (Mnari-Hattab et al., 2015). A new virus-like disease was observed in the zucchini (*C. pepo L. hybrid Linea F1*) crops in Ileia and Messinia regions in southeastern Greece during the autumn season of 2018 (Orfanidou et al., 2019). Now, this virus is fully dispersed and founded in all Asian, North African, and Southern European countries. In 2018, when ToLCNDV was discovered in Apulia in marketable fields of zucchini squash, growers had good reason to be concerned about its recurrent outbreaks. The chayote plants infected by ToLCNDV showed yellow spots, leaf curling, yellow mosaic, puckering and enations, and also reduced the fruit's quality. Fruits harvested from infected plants were malformed and were unable to be sold in the market. A new strain of ToLCNDV with the identity of 91-92% with other ToLCNDV isolates was assigned as

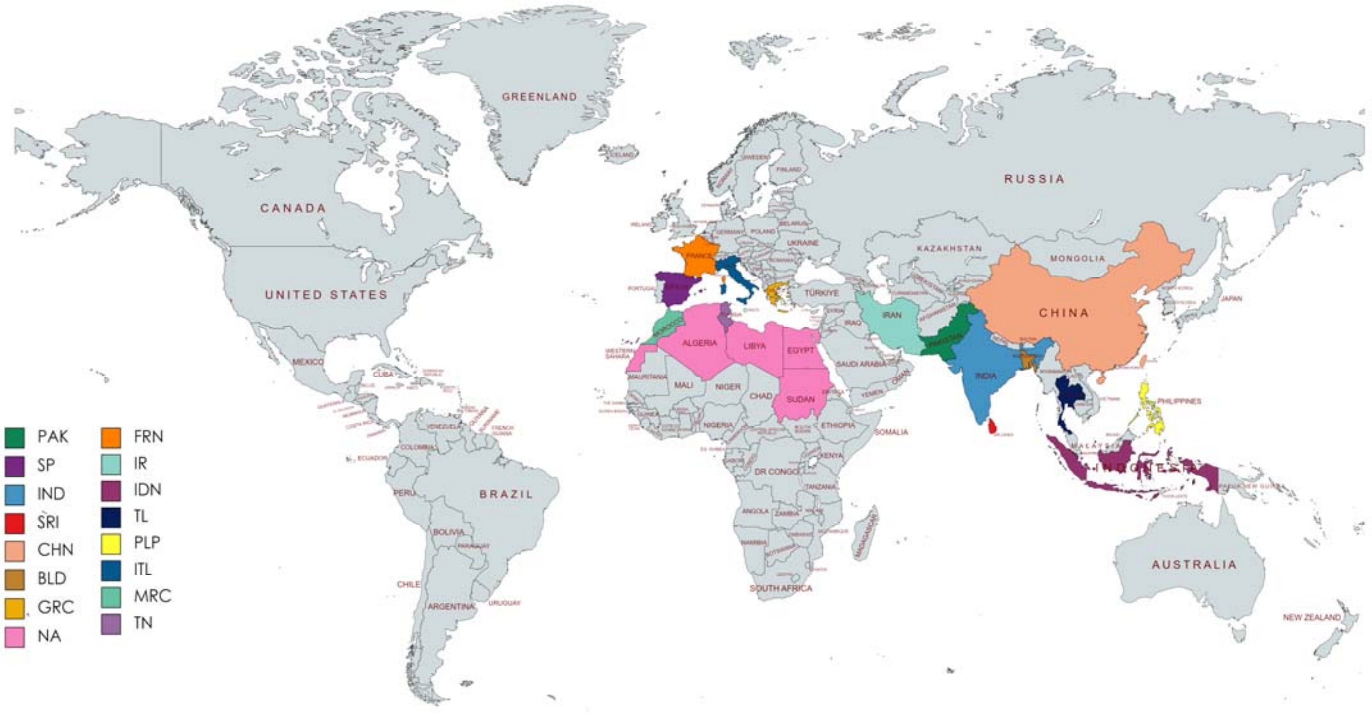

Figure 2. *The geographical distribution of Tomato Leaf Curl New Delhi Virus (ToLCNDV) is illustrated on the map, showcasing distinct colors to represent various nations that have been impacted worldwide, each corresponding to a unique alphabetical symbol assigned. PAK(Pakistan), SP(Spain), IND(India), SRI(Sri Lanka), CHN(China), BLD(Bangladesh), GRE(Greece), NA(North Africa), FRN(France), IR(Iran), IDN(Indonesia), TL(Thailand), PLP(Philippines), ITL(Italy), MRC(Morocco) and TN(Tunisia).*

the cause of this disease, qualifying to be considered as a divergent strain. The phylogenetic analysis revealed that the sequences of DNA-A isolated from ridge gourd, chayote, and ash gourd cultivated in India shared a common origin with the isolates of ToLCNDV reported from Spain. This contrast between the isolates shows the genetic diversity and origin of the isolates.

Host range

According to European and Mediterranean Plant Protection Organization (EPPO), the new host range of ToLCNDV increases annually (Moriones et al., 2017). In Turkey, zucchini squash is considered an important horticultural crop producing an estimated 6230 tonnes in an area of 19950 ha in 2022 (Istat, 2021). However, a variety of viruses, most notably ToLCNDV, have consistently attacked this crop in recent years. The two most significant crops in Italy that are impacted by this virus are tomato and zucchini squash. This virus poses a particular hazard to zucchini squash, a cucurbitaceous crop. The prominent symptoms of zucchini squash infected by ToLCNDV, are leaf curling, swelling of veins of new leaves, reduced internodal distance, yellow mosaic in fresh leaves, ridges on the skin of fruit along with reduced size (Panno et al., 2019) which ultimately resulted in less acceptance in the market. Fruit showing the symptoms of rough peel, long cracking, and reduced size. The mature fruits are affected and surface roughness is observed reducing the marketability of that fruit. Regarding susceptibility, young seedlings are particularly susceptible to the disease (Padidam et al., 1995; Ruiz et al., 2015). The cucumber plant shows yellowy-green mosaic symptoms on the leaves (Mizutani et al., 2011). This virus was reported to infect chilli grown in the open fields in Lucknow, Uttar Pradesh, India (Khan et al., 2006). In August 2022, samples showing symptoms of yellowish greening, severe curling of leaves, mosaic, and stunting and were found to be infected with ToLCNDV which was confirmed by molecular phylogeny analysis and construction of infectious clones (Zeng et al., 2023). Chayote (*Sechium edule*) is mainly grown for its fruit and shows different types of symptoms in hilly areas of Tamil Nadu. The disease incidence percentage was 50.3–100% and yield losses were about 69.9% in the Dindigul district. The fruits of diseased plants were malformed and were not marketable (Sangeetha et al., 2018). The ToLCNDV-ES genome titers that appear are substantially lower in tomato plants than in zucchini plants, which may be related to the differences in how the virus manifests its symptoms, is detectable, and spreads (Simón et al., 2018). ToLCNDV was reported to infect tomatoes and almost all crop plants in the Cucurbitaceae family. In weeds, three species including *Datura stramonium*, *S. nigrum* and *Sonchus oleraceus* were identified as alternative host plants of ToLCNDV, which were supposed to be a bridge between the growing seasons and may provide viral inoculum on the onset of cropping time (Juárez et al., 2019). On the whole Indian subcontinent, *Eclipta prostrata* is a typical weed along waterways. This plant frequently displays yellow vein signs that are indicative of specific begomoviruses. Total DNA taken from infected *E. prostrata* leaf samples collected from Punjab, Pakistan was subjected to PCR analysis, and the results showed that the virus was a strain of ToLCNDV (Haider et al., 2006).

Transmission methods

A number of diseases affecting vegetable crops are transmitted by hemipterans like leaf hoppers, aphids and plant hoppers as sucking insects, the most of diseases are viral diseases of the genus Begomovirus, the largest virosphere with 409 recognized species (Fiallo-Olivé et al., 2021). The begomoviruses are generally phloem-limited viruses transmitted in a persistent and circulative manner by *Bemisia tabaci* as a vector (Rosen et al., 2015). The whitefly *B. tabaci Gennadius*, which is extensively present in tropical and subtropical countries as well as in the Mediterranean basin, and itself poses a serious danger to many cultivated crops, is the carrier of the ToLCNDV (Sharma & Prasad, 2017). Three different Italian ToLCNDV isolates were effectively transferred by mechanical inoculation to melon, zucchini squash, and cantaloupe (Panno et al., 2019). Furthermore, it was confirmed by López and co-workers that the mechanical transmission of ToLCNDV was successful in germplasm breeding of the Cucurbitaceae family in 4 genera and 13 species showed tolerance to the mechanical transmission of ToLCNDV, was found in melon, within *Cucumis melo subsp. agrestis var. momordica* and in wild agrestis accessions (López et al., 2015). Most of the isolates of ToLCNDV are not mechanically transmitted to their host plants. There is a single isolate known as ToLCNDV oriental melon (OM), which was originally isolated from an infected oriental melon plant, can be mechanically transmissible (Chang et al., 2022) and this transmission is demonstrated to be associated with the movement protein (MP) of DNA-B. A multifunctional protein called viral MP helps viruses spread from cell to cell and throughout the body. The nuclear entrance of ToLCNDV is facilitated by MP, which participates in begomoviral intracellular trafficking, and indirectly collaborates with nuclear shuttle protein (NSP). According to reports, MP functions as both a virulence and host range determinant. ToLCNDV spreads systemically, but the presence of viruses is more common in leaves than in flowers. The sap transmission of this virus was successful for some selected cucurbitaceous hosts (Sangeetha et al., 2018). On a farm in Giugliano, Campania, Naples, Italy, in 2017, ToLCNDV was discovered in young seedlings that had by itself sprouted from fruits that had fallen the year before. These findings raise the possibility that the seeds play a role in the virus's vertical transmission, that's why there should be measures to overcome this possibility. In order to determine if ToLCNDV may be transferred from zucchini squash seeds to younger plants, seeds from two cultivars of the squash with the virus were gathered in Naples in 2017 and 2018. These seeds were used to grow one to three-week-old seedlings from which viral DNA of ToLCNDV was amplified using a specific primer set. All collected seeds tested positive for viral contamination by PCR, and 61.36% of analyzed seedling samples tested positive for viral spread. In

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order to show that seedlings from ToLCNDV-infected seeds did serve as an inoculum, mechanical transmission from seed-borne virus-infected seedlings to healthy zucchini squash plants was also done successfully (Kil et al., 2020). Pre-miRNA and miRNA targets in flowers have been the subject of expression investigations, which have shown that the majority of these transcripts do not express at levels corresponding to those seen in leaf tissues. However, ToLCNDV agro-infected plant blooms display the disease symptoms. Furthermore, the transcriptome of leaf tissues is drastically altered after ToLCNDV infection since they are the main site for viral entry. So, it is not unexpected that the deregulation of ToLCNDV-induced transcript is still mostly localized in the tissues of the leaves (Naqvi et al., 2010).

Detection methods

Serological and molecular approaches are being used for the identification of ToLCNDV (Figàs et al., 2017) and commercial (Agdia, Elkhart, IN, USA), lateral flow ImmunoStrip® (LFA) is available, while end-point PCR is one of the molecular techniques (Panno et al., 2019), besides rolling circle amplification PCR (RCA-PCR) (Jeevalatha et al., 2014), real-time PCR (Luigi et al., 2020), nucleic acid spot hybridization (NASH) using specific riboprobes, colorimetric loop-mediated isothermal amplification (LAMP) (Naganur et al., 2019), LAMP-coupled CRISPR–Cas12a (Mahas et al., 2021), and a commercial ready-to-use real-time LAMP kit combined with proprietary devices (i.e., an ICGENE ToLCNDV diagnostic kit). A number of assays like Dot Immuno Binding Assay (DIBA), Western Blotting (WB), Direct Antigen Coating Enzyme Linked Immuno Sorbent Assay (DAC-ELISA), Immuno Capture Polymerase Chain Reaction (IC-PCR), and Immuno Capture Loop-Mediated Isothermal Amplification (IC-LAMP), were used to successfully identify a 30.5 kDa ToLCNDV-Rg-CP (Naganur et al., 2023).

Economic losses

Two different strains of ToLCNDV are responsible to be the reason of leaf curling disease in tomato crop in India. The reported yield losses ranged from 17.6% to 99.7% depending on the time of infection, disease incidence and disease severity (Rao & Reddy, 2020). Singh and Sastry (1973) testified 92.3% losses, in 30 days of tomato seedling infected by ToLCNDV. Chayote (*Sechium edule*) is mainly grown for its fruit and shows different types of symptoms in hilly areas of Tamil Nadu. The disease incidence percentage was 50.3–100% and yield losses were about 69.9% in the Dindigul district. The fruits of diseased plants were malformed and were not marketable (Sangeetha et al., 2018). Muniyappa and Saikia (1989) conveyed that there is more yield loss in winter-grown crops that ranges from 52.5-100%, as compared with summer-grown crops that range from 6.4 to 52.2%. The yield losses vary in a range of 17.6-99.7%, depending on infection, severity, and incidence (Rao & Reddy, 2020).

Prevailing strains and their management

In 2012, a new strain known as ToLCNDV-ES was first introduced in Spain and it severely damaged zucchini crop harvests. The minimum acquisition access and inoculation access periods were similar in tomato and zucchini plants infected by ToLCNDV-ES strain (Janssen et al., 2022). On the universal host plant (*Nicotiana benthamiana*) and Oriental Melon plant, a viral culture known as SL-1 that was extracted from the diseased melon was inoculated through mechanical inoculation. SL-1 didn't respond to antibodies in contrast to DNA viruses that infect cucurbits. The isolated viral genomic DNA was then amplified using degenerate primers designed for begomoviruses. DNA-A and DNA-B of SL-1 genomic sequence revealed 97.7% and 90.6% of nucleotides correspondingly which shared the most similarities with nucleotides of a cucumber isolate of ToLCNDV. The virus isolate SL-1 was named as *Tomato Leaf Curl New Delhi Virus* oriental melon isolate (ToLCNDV-OM) (Chang et al., 2010).

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Implementation of preventative measures is fundamentally the foundation of virus disease management. ToLCNDV infections have to be kept to a minimum, in this situation in order to effectively control whiteflies. Some methods include adult bulk trapping, parasitoid/predator releases, insect-proof nets, and selective pesticides (Rapisarda et al., 2005); moreover, to stop the virus from spreading to the entire crop and reducing the inoculum, it is crucial to eliminate symptomatic plants. The agriculture industry is continuously under pressure to boost crop yields and resource utilization effectiveness due to the growing global population. Despite the fact that their active components are frequently persistent pollutants in soil and wastewater and hazardous to a variety of creatures, pesticides and fertilizers are nonetheless routinely used to meet necessary production requirements. A number of technical advancements and environmentally acceptable agrochemical substitutes have been suggested during the past three decades to increase the importance of agriculture and lessen its negative effects on human health and ecosystems (Rouphael & Colla, 2020). Natural wild plant biostimulants are getting interest as new products that enhance plant growth (Ugena et al., 2018). Practically, these botanical products contribute to growth, fruit set, flowering, nutrient use efficiency and productivity as well as to tolerance against a wide range of abiotic stresses (Colla & Rouphael, 2015). In 2018, when ToLCNDV was discovered in Apulia in marketable fields of zucchini squash, growers had good reason to be concerned about its recurrent outbreaks. Consequently, it is necessary to use prolonged and environmentally friendly strategies. *Luffa cylindrica* and *C. moschata* have genetic resistance, however, grafting is considered as a more rapid and adaptive option than genetic resistance as the graft injury produces tolerance rather than resistance to airborne viral infection. At the expense of plant growth, primary metabolism and development, resistance genes require the mobilization of energy resources, in contrast to tolerance (Mastrochirico et al., 2022). Similar to many other plant viruses, the most effective and productive management technique for reducing begomoviruses like ToLCNDV is the establishment of genetic resistance in the host plant (Lapidot et al., 2002). The potential of viruses to develop and overcome resistant features makes it vital to keep in mind that depending entirely on the continuing usage of resistance for sustainable control of ToLCNDV may be compromised (García-Andrés et al., 2009). The danger of resistance break could be reduced by combining virus resistance with other control methods in management approaches in order to obtain a more durable control (Seal et al., 2006).

Author Contributions

MT Shakeel conceptualized the study. M Raheel and AR Khan performed literature search. A Majid wrote and prepared the original draft. A Moosa, W Ashraf and A Maqsood participated in the article review and editing. MU Shafiq contributed to graphic design. MN Aslam provided overall supervision. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement

All data is available and present in the publication.

Conflict of Interest

The authors declare no conflict of interest.

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