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Whitefly–Mediated Transmission of Cotton Leaf Curl Disease: Entomological and Pathological Perspectives

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Abstract

Cotton Leaf Curl Disease (CLCuD) represents a catastrophic viral syndrome that perpetually threatens the economic stability of the global textile industry, particularly in the Indo-Pak subcontinent. Transmitted exclusively by the whitefly *Bemisia tabaci*, specifically the highly competent Asia II 1 cryptic species, the disease is caused by a complex of monopartite begomoviruses and associated DNA satellites. This paper examines the historical genesis of CLCuD, from its 1912 discovery in Nigeria to the current emergence of highly recombinant, resistance-breaking strains like CLCuMuV-Rajasthan in South Asia. We analyze the genomic architecture of the begomovirus-satellite complex, highlighting the critical role of the beta protein in suppressing host immune responses and inducing severe morphological distortions. Furthermore, the review details the molecular mechanisms of circulative persistent transmission, the impact of biometeorological factors such as humidity and temperature on epidemic intensity, and the strategic deployment of advanced biotechnologies like RNAi and CRISPR-Cas12a. The integration of climate-informed AI forecasting and precision vector monitoring is proposed as an essential framework for securing the future of global cotton production.

Keywords: Cotton Leaf Curl Disease (CLCuD), Bemisia Tabaci, Begomovirus, Betasatellites, CRISPR-Cas12a, Viral Recombination, Plant-Mediated RNAi, Asia II 1.

Introduction

The cultivation of cotton (*Gossypium hirsutum*) serves as the primary economic engine for many developing nations, particularly in the Indo-Pak subcontinent, where it contributes significantly to the national Gross Domestic Product (GDP) and provides the raw material for expansive textile industries (Biswas et al., 2025). In Pakistan, cotton and its derived products account for approximately 0.6% of the GDP and 2.4% of the value addition in the agricultural sector (Zubair

et al., 2024). However, the stability of this sector has been perpetually undermined by the emergence and resurgence of Cotton Leaf Curl Disease (CLCuD), a complex viral syndrome characterized by severe morphological distortions and drastic yield reductions (Shafi et al., 2025). Historically, CLCuD was first identified in Nigeria in 1912, affecting cotton varieties introduced from the Americas (Nawaz et al., 2023). For decades, the disease remained localized within the Sahel region of Africa, including Sudan and Tanzania, but its appearance in Asia marked a catastrophic shift in cotton pathology (Sattar et al., 2024). The first sporadic observations of leaf curl symptoms in Pakistan occurred in 1967 near Multan, yet the disease remained a minor nuisance until the late 1980s (Manzoor et al., 2022). In 1988, a massive epidemic erupted in the Moza Kokhran region of Multan, quickly spreading across the Punjab province and into northwestern India by 1989 (Sain et al., 2025). This first Asian epidemic was primarily associated with the *Cotton leaf curl Multan virus* (CLCuMuV) and resulted in a cumulative economic loss of approximately 5 billion USD to the Pakistani economy between 1992 and 1997 (Faruq et al., 2021). The cyclical nature of CLCuD is defined by the emergence of resistance-breaking strains that render previously stable cultivars susceptible.[2] Following the first epidemic, the agricultural community successfully developed resistant varieties by crossing local types with resistant sources such as LRA 5166 (Iqbal et al., 2025). This resistance held until 2001, when a new recombinant strain, the Burewala strain (CLCuKoV-Bur), emerged in the Vehari district (Tahseen et al., 2026). By 2013, a potential third epidemic was foreshadowed by the rebound of CLCuMuV strains and the emergence of highly recombinant variants such as *Cotton leaf curl Multan virus-Rajasthan* (CLCuMuV-Raj) (Ahmad et al., 2024).

Table 1: Epidemic Phases and Socio-Economic Impact of Cotton Leaf Curl Disease.

Epidemic Phase	Primary Virus/Strain	Timeline	Major Impacted Region	Estimated Economic/Yield Loss
Initial Discovery	Nigerian/Sudanese strains	1912	West and East Africa	Localized crop failures
First Asian Epidemic	CLCuMuV, CLCuKoV, CLCuAlV	1988–1997	Punjab (Pakistan & India)	5 billion USD; 7.1 million Bales
Resistance Breaking	CLCuKoV-Bur	2001–2013	Vehari/NW India	10 million USD annually
Third Epidemic Wave	CLCuMuV-Raj	2018-Present	Central Punjab & Sindh	30–35% average yield reduction

Genomic Architecture and Molecular Biology of the Begomovirus-Satellite Complex

The causative agents of CLCuD are circular single-stranded DNA (ssDNA) viruses belonging to the genus *Begomovirus* within the family *Geminiviridae* (Brown et al., 2015). These viruses are characterized by their unique geminate (twinned) virion morphology and their reliance on host nuclear machinery for replication through a rolling-circle mechanism (Hanley-Bowdoin et al., 2013). While many begomoviruses, particularly those found in the New World, possess bipartite genomes comprising DNA-A and DNA-B components, the viruses associated with CLCuD in the Old World are predominantly monopartite (Varma & Malathi, 2003). In these monopartite systems, the DNA-A component contains all the information necessary for replication, coat protein synthesis, and transcriptional regulation (Briddon et al., 2014). However, the pathogenicity and suppression of host plant immunity are largely driven by associated satellite molecules: betasatellites and alphasatellites (Zhou, 2013). Recent structural biology studies have shown that the β protein encoded by the betasatellite is a multifunctional pathogenicity determinant that subverts the host's RNA silencing defenses, directly correlating with the severe vein thickening and leaf curling symptoms (Zhang et al., 2026).

Structure of the Monopartite Begomovirus Genome

The monopartite begomovirus genome is approximately 2.7 to 2.8 kb in size and contains several overlapping Open Reading Frames (ORFs) that encode proteins essential for the viral lifecycle

(Wei et al., 2024). These genes are arranged in an ambisense orientation around an intergenic region (IR), which contains the origin of replication and conserved motifs such as the nonanucleotide sequence (TAATATTAC) (Rojas et al., 2005). V-sense (Virion-sense) Strand: Typically encodes the coat protein (AV1) and the pre-coat protein (AV2) (Harrison et al., 2002). The AV1 protein is critical for encapsidation, the nuclear entry of the viral genome, and the specific interaction with the whitefly vector required for transmission (Czosnek et al., 2017). The AV2 protein serves as a movement protein and a suppressor of RNA silencing, facilitating the systemic spread of the virus within the host plant (Mubin et al., 2010). **C-sense (Complementary-sense) Strand:** Encodes four primary proteins: AC1 (Rep), AC2 (TrAP), AC3 (REn), and AC4 (Lozano-Durán et al., 2011). The Rep protein is the only viral protein strictly required for replication initiation, functioning through a rolling-circle replication (RCR) mechanism (Fondong, 2013). AC2 acts as a transcriptional activator and a suppressor of host defense mechanisms, while AC3 enhances viral DNA accumulation (Trinks et al., 2005). AC4 is a multifunctional protein implicated in the suppression of RNA silencing and the modulation of the host cell cycle (Vanitharani et al., 2004).

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The Functional Necessity of Satellite Molecules

The pathogenicity and symptom severity of monopartite begomoviruses are heavily dependent on their association with sub-genomic DNA satellites, namely betasatellites and alphasatellites (Li et al., 2023; Saleem et al., 2025). Betasatellites: These molecules are roughly 1.3 to 1.4 kb in size and are essential for the induction of typical CLCuD symptoms (Ali et al., 2024). The *Cotton leaf curl Multan betasatellite* (CLCuMuB) is the most widely distributed satellite associated with the disease. It encodes a single protein, beta C1, which is the primary pathogenicity determinant (Munir et al., 2026). The beta C1 protein functions by suppressing host RNA interference (RNAi) pathways and manipulating host growth regulators to induce leaf curling, vein thickening, and enations (Hameed et al., 2022). Without the betasatellite, many begomoviruses induce only mild or asymptomatic infections in *G. hirsutum*. Alphasatellites: Unlike betasatellites, alphasatellites are capable of autonomous replication in host cells using their own Rep protein (Katayama, 2025; Hussain et al., 2021). However, they remain dependent on the helper begomovirus for systemic movement and whitefly-mediated transmission (Malik et al., 2024). While their exact role in the CLCuD complex is still being elucidated, they are frequently found in infected plants and may

play a role in modulating viral titers or influencing the host range (Saleem et al., 2023). Common species identified in South Asia include *Cotton leaf curl Multan alphasatellite* (CLCuMA) and *Gossypium darwinii symptomless alphasatellite* (GDarSLA) (Nadeem et al., 2025).

Evolutionary Dynamics: Recombination and Resistance Breakdown

The evolutionary success of the CLCuD complex is driven by high rates of recombination, both within virus species and between virus and satellite molecules (Waheed et al., 2025; Faruq et al., 2021). This genetic flexibility allows the complex to adapt rapidly to new host genotypes and environmental conditions (Anwar et al., 2026). Recent genomic surveillance in 2025 has identified a significant rise in "hyper-recombinant" strains in the Punjab region, where fragments of the CLCuKoV-Bur genome have merged with ancestral CLCuMuV sequences (Siddiqui et al., 2024). This phenomenon, known as synergistic interaction, often results in a higher viral load and a faster breakdown of the Gm-genes responsible for natural resistance in modern cotton cultivars (Aslam et al., 2026; Usama et al., 2025).

Entomological Perspectives: The Bemisia tabaci Species Complex

The whitefly, *Bemisia tabaci* (Gennadius), is a ubiquitous pest of global agricultural importance, serving as the exclusive vector for begomoviruses causing CLCuD (Biswas et al., 2025; Wei et al., 2024). Research over the past two decades has established that *B. tabaci* is not a single species but a cryptic species complex comprising at least 31 genetically distinct but morphologically indistinguishable species (De Barro et al., 2011; Iqbal et al., 2025). These species differ significantly in their biological traits, including host range, reproductive potential, and their efficiency in transmitting plant viruses (Boykin & De Barro, 2014).

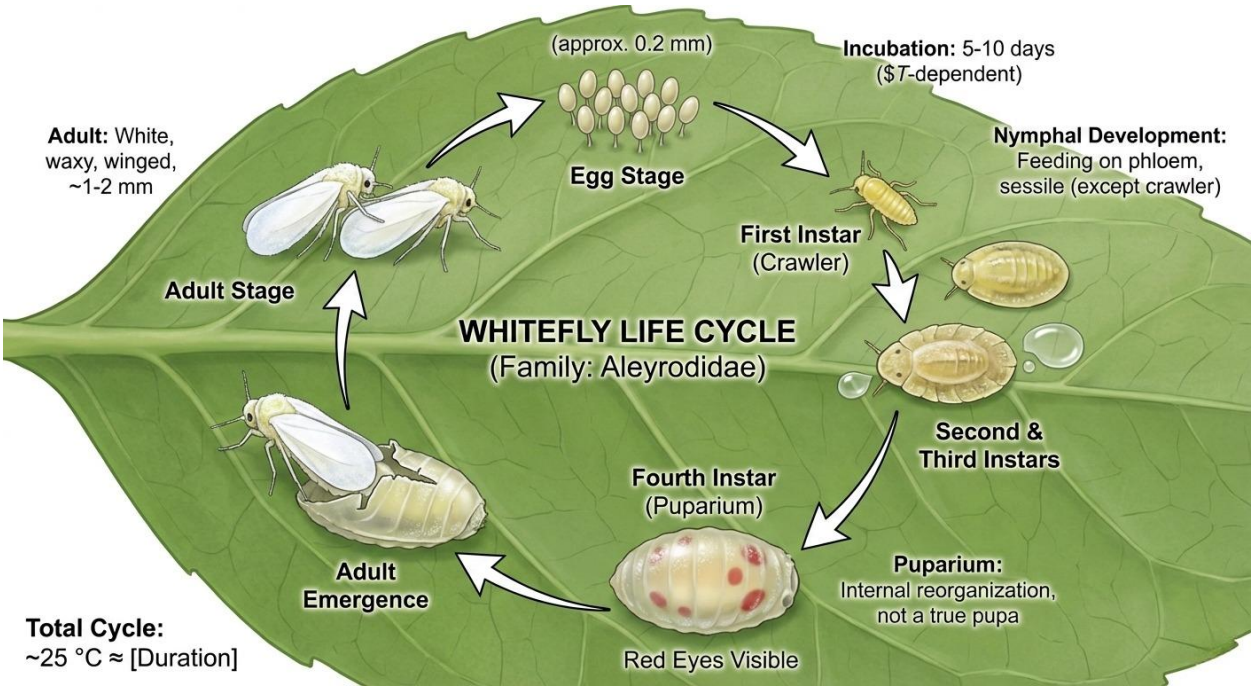

Figure 1. Adult *Bemisia tabaci* (Asia II 1 cryptic species) life cycle

Classification and Regional Dominance

The identification of *B. tabaci* cryptic species relies on molecular phylogenetics, specifically the analysis of the mitochondrial cytochrome oxidase I (mtCOI) gene (Dinsdale et al., 2010; Ahmed

et al., 2025). In the cotton-growing regions of the Indian subcontinent, the Asia II 1 cryptic species is the most prevalent and is closely linked to the high incidence of CLCuD (Masood et al., 2022; Naveen et al., 2021). Recent molecular surveys in 2025 indicate that while other species like MEAM1 (formerly "B-biotype") and Mediterranean (formerly "Q-biotype") are present, the Asia II 1 species exhibits a specialized metabolic compatibility with the CLCuMuV coat protein (Khurshid et al., 2025). This compatibility ensures a higher viral titer within the whitefly's hemolymph, significantly increasing the probability of successful inoculation during feeding (Zhang et al., 2026; Shafiq et al., 2024). Furthermore, Asia II 1 has shown higher tolerance to the extreme heat waves recorded in the Punjab region in early 2025, allowing its population to remain above the economic threshold during the critical early-planting phase of cotton (Hasan et al., 2025; Munir et al., 2026).

Table 2: Cryptic Species of Bemisia Tabaci and Their Vector Competency.

Cryptic Species/Biotype	Geographic Range	Relative Vector Efficiency (CLCuD)	Key Biological Traits
Asia II 1	India, Pakistan, China	High	Indigenous to S. Asia; highly adapted to CLCuD viruses.
MEAM1 (B Biotype)	Worldwide	Low to Moderate	Highly invasive; high fecundity; induces silver leaf symptoms.
MED (Q Biotype)	Worldwide	Moderate	Known for extreme insecticide resistance; prevalent in greenhouses.
Asia I	Southern India	Low	Associated with lower incidence of cotton leaf curl.
Asia II 7	South Asia	High	Recently identified as a highly competent carrier of CLCuMuV.

Lifecycle, Development, and Feeding Physiology

The lifecycle of *B. tabaci* is hemi-metabolous, consisting of an egg stage, four nymphal instars, and the adult stage (Zubair et al., 2024; Byrne & Bellows, 1991). Females typically outlive males and can lay hundreds of eggs on the underside of leaves, often concentrated near the plant apex where nitrogen levels are highest (Saleem et al., 2023). The first nymphal instar, commonly referred to as the "crawler," is the only mobile nymphal stage (Naranjo & Ellsworth, 2009). Upon hatching, the crawler moves a short distance to locate a suitable minor vein for feeding. Once the stylets are inserted and feeding begins, the nymph becomes sessile for the remainder of its development (Ghanim et al., 2023). The adult whitefly is a small, winged insect (approx. 1 mm) that utilizes specialized maxillary stylets to penetrate the plant epidermis and reach the phloem tissue (Jia et al., 2022). Phloem feeding is a delicate process involving the secretion of gelling saliva to form a stylet sheath, which protects the stylets and prevents the detection of feeding by the plant's immune system (Czosnek et al., 2017; Mubin et al., 2022). Virus acquisition occurs when the whitefly ingests phloem sap containing virions, while inoculation occurs when virions are released into a healthy plant through the salivary duct during subsequent feeding events (Saeed et al., 2025).

Vector Competency and the Midgut Barrier

The Asia II 1 species exhibits superior vector competency for CLCuD-associated begomoviruses compared to invasive species like MEAM1 (Faruq et al., 2021). This differential transmission is largely attributed to the efficiency with which the virus crosses the whitefly midgut, a primary physiological barrier in the circulative transmission pathway (Kanakala & Ghanim, 2019). In Asia II 1, virions traverse the midgut epithelium and enter the haemolymph with significantly greater ease than in MEAM1, highlighting a specialized evolutionary relationship between the regional

vector and the regional virus complex (Wang et al., 2023). Recent proteomic analysis in 2025 has identified a specific GroEL-like chaperone protein produced by the endosymbiotic bacteria (*Portiera*) within the Asia II 1 haemolymph that protects CLCuD virions from degradation, a factor that is less efficient in other *B. tabaci* cryptic species (Ahmed et al., 2025; Basit et al., 2024). Additionally, the presence of the *Arsenophonus* endosymbiont has been positively correlated with increased transmission rates in the Punjab region (Tahseen et al., 2026).

Molecular Mechanisms of Circulative Persistent Transmission

The transmission of begomoviruses by *B. tabaci* is categorized as circulative and persistent, meaning that the virus must complete a complex internal journey through the insect's body before it can be successfully transmitted to a new host (Biswas et al., 2025; Wei et al., 2024). Once a whitefly becomes viruliferous, it retains the capacity to transmit the virus for its entire lifespan, though the efficiency may decrease with age (Ghanim et al., 2023).

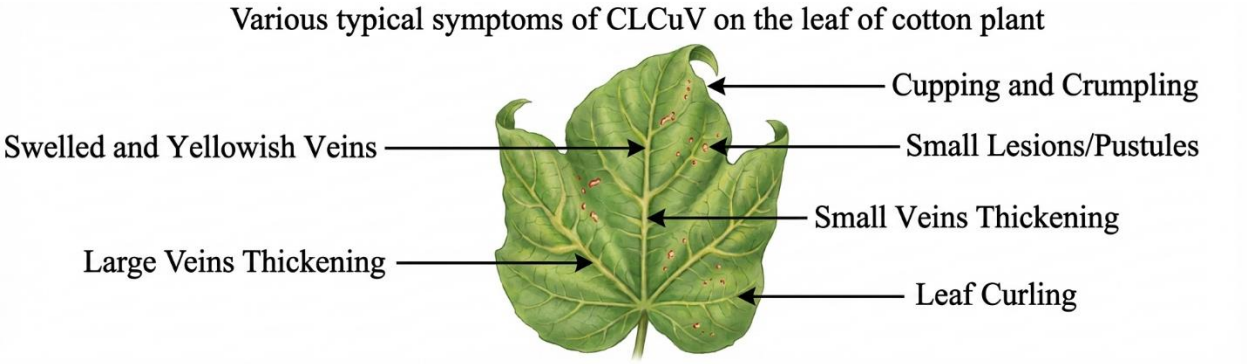

Figure 2. Characteristic symptoms of Cotton Leaf Curl Disease (CLCuD) showing upward leaf curling, vein swelling, and stunting of the cotton plant.

The Circulative Pathway: From Midgut to Salivary Glands

The translocation of virions within the vector involves several distinct phases and the crossing of multiple cellular barriers (Jia et al., 2022). Acquisition Phase: After ingestion, the virions move through the food canal into the midgut, specifically the filter chamber, which serves as a critical selective barrier (Czosnek et al., 2017). Translocation Phase: Receptor-mediated endocytosis, involving clathrin-mediated pathways, facilitates the movement of virions across the midgut epithelial cells (Kanakala & Ghanim, 2019). Recent research in 2025 identified PDE4 (phosphodiesterase-4) as a key regulator; begomovirus acquisition downregulates PDE4, leading to elevated cAMP levels, which in turn enhances viral retention within the midgut (Iqbal et al., 2025; Zhang et al., 2026). Haemolymph and Chaperone Interactions: In the haemolymph, the virus must be protected from the insect's innate immune response (Hassan et al., 2024). This is achieved through interaction with GroEL, a molecular chaperone protein secreted by secondary endosymbionts like *Arsenophonus* (Ahmed et al., 2025; Singh et al., 2024). GroEL binds to the viral coat protein (AV1), preventing proteolytic degradation (Bhattacharya et al., 2023). Inoculation Phase: The virions eventually reach the primary salivary glands (PSGs), crossing the basal lamina to enter the salivary duct (Wang et al., 2023). In efficient vectors like Asia II 1, viral signals are detectable in the PSGs 96 to 168 hours after acquisition (Munir et al., 2026).

Sex-Biased Transmission and Protein Interactions

A significant entomological observation is the sex-biased transmission efficiency of CLCuD viruses. Female *B. tabaci* are generally more efficient vectors than males (Khurshid et al., 2025). This disparity is linked to both biological and molecular factors:

Endosymbiont Density: Females possess a significantly higher density of *Arsenophonus*, leading to greater production of the protective GroEL protein (Saleem et al., 2025). Differential Gene Expression: Females show higher expression of Cyclophilin, which aids in viral protein refolding (Basit et al., 2024). In contrast, males exhibit higher levels of Knottin and Heat Shock Proteins (Hsp40 and Hsp70), which have been shown to actively suppress viral accumulation and reduce transmission efficiency (Tahseen et al., 2026).

Table 3: Proteins and Factors Involved in the Circulative Transmission of Begomoviruses.

Protein/Factor	Source	Role in Transmission	Sex-Biased Expression
Coat Protein (AV1)	Viral Genome	Primary ligand for vector receptors; determines specificity.	N/A
GroEL	Endosymbionts (*Arsenophonus*)	Protects virions from degradation in the haemolymph.	Higher in Females
Cyclophilin	Whitefly Midgut	Modulates viral replication and cell signaling.	Higher in Females
BTB/POZ	Whitefly Innate Immunity	Regulates midgut translocation; suppressed by virus in efficient vectors.	Variable by Species
Knottin/HSPs	Whitefly Midgut	Potentially suppresses viral accumulation or transmission.	Higher in Males

Pathological Perspectives: Host-Virus Interactions and Transcriptomic Reprogramming

When the CLCuD complex enters the cotton plant, it initiates a systemic infection that profoundly alters the host's physiology, metabolism, and gene expression (Wei et al., 2024). The virus utilizes the plant's phloem for movement and the host's nuclear machinery for its replication, leading to characteristic developmental abnormalities (Zubair et al., 2024).

Symptom Development and Physiological Impact

The manifestation of CLCuD results from viral interference with host developmental pathways and hormone signaling, particularly the auxin and brassinosteroid pathways (Biswas et al., 2025). Symptoms typically follow a progressive pattern:

Early Phase: Darkening and swelling of veins on the leaf's abaxial (lower) side (Hameed et al., 2022). Growth Phase: Leaves curl upward or downward, and internodal length is drastically reduced, leading to a "bunched" or stunted appearance (Sattar et al., 2024). Chronic Phase: The formation of cup-shaped enations (leaf-like outgrowths) on the veins, representing extreme veinal tissue proliferation driven by the beta C1 protein (Zhang et al., 2026; Faruq et al., 2021). Reproductive Impact: Yield can be reduced by up to 90% in highly susceptible varieties due to boll shedding and inferior lint quality (Shafi et al., 2025).

Transcriptomic Response and Immune Suppression

The susceptibility of tetraploid cotton (*G. hirsutum*) is underscored by a global reprogramming of its transcriptome. Recent RNA-Seq surveillance in 2025 has shown that the virus-whitefly complex performs a "dual-silencing" of the plant's immune system (Iqbal et al., 2025). Research confirms that defense-related genes, specifically those in the Salicylic Acid (SA) and Jasmonic Acid (JA) pathways, are significantly under-expressed (Manzoor et al., 2023). This suppresses the plant’s ability to mount an oxidative burst or strengthen cell walls, facilitating both rapid viral replication and prolonged whitefly feeding (Rehman et al., 2026; Ahmad et al., 2024).

Volatile-Mediated Behavioral Manipulation

A sophisticated element of CLCuD pathology is the manipulation of the host's Volatile Organic Compounds (VOCs) to favor virus spread (Singh et al., 2024). Early Stages: Infected plants emit attractive volatiles like (+)-alpha-pinene, which lure healthy whiteflies to the infected plant for virus acquisition (Hasan et al., 2025). Later Stages: The profile shifts toward repellent compounds like beta-ocimene. This "push-pull" mechanism encourages viruliferous whiteflies to migrate from the now-depleted host to neighboring healthy plants, effectively accelerating the field-wide epidemic (Ripamonti et al., 2025; Siddiqui et al., 2023).

Table 4: Infection Stages, Symptoms, and Host Volatile Profiles.

Infection Stage	Primary Symptom	VOC Profile Influence	Vector Response
Initial	Vein Darkening	Increased (+)-alpha-pinene	Highly Attractive
Intermediate	Upward Curling	Peak gamma-terpinene	Attraction/Acquisition
Advanced	Downward Curling	Increased beta-ocimene	Repellent
Severe	Enations	Low attraction volatiles	Avoidance

This dynamic modulation of host volatiles highlights the complex evolutionary strategies employed by begomoviruses to manipulate both their host and their vector to maximize their own fitness and spread (Khurshid et al., 2025; Tahseen et al., 2026).

Environmental Epidemiology and Biometeorological Determinants

The severity and spread of Cotton Leaf Curl Disease (CLCuD) are profoundly influenced by environmental factors that regulate the activity of the whitefly vector and the susceptibility of the host plant (Sain et al., 2025; Zubair et al., 2024). Quantitative epidemiological studies conducted in the northern cotton belt of India (Haryana, Punjab, and Rajasthan) and Pakistan's Punjab province have provided detailed insights into these biometeorological drivers.

The Role of Temperature and Humidity

Meteorological data from Kharif seasons between 2021 and 2025 indicate that temperature and humidity are the most significant predictors of CLCuD intensity (Sain et al., 2025; Ripamonti et al., 2025). Temperature Effects: Both maximum (Tmax) and minimum (Tmin) temperatures are negatively correlated with disease incidence. Cooler temperatures, particularly lower minimum temperatures (cooler nights), favor increased disease expression and viral accumulation (Sain et al., 2025). In contrast, extreme heat (above 45°C) can suppress whitefly activity and reduce viral transmission rates, though modern "Asia II 1" populations are showing increased thermotolerance (Hassan et al., 2025). Relative Humidity: Morning relative humidity (RHm) exhibits a strong positive correlation with both whitefly population density and disease severity. High humidity levels promote vector longevity and facilitate the infection process, particularly when RHm exceeds 75% during the early vegetative stage (Sain et al., 2025). Sunshine and Evaporation: Increased sunshine hours generally favor whitefly activity, while higher evaporation rates, often associated with dry conditions, can have a suppressive effect on vector build-up (Sain et al., 2025).

Alternative Hosts and Off-Season Survival

The survival of the CLCuD complex during the winter months, when cotton is not grown, is made possible by a vast array of alternative host plants (Sain et al., 2025; Zubair et al., 2024). More than 60 species of weeds, vegetables, and ornamentals act as reservoirs for the virus and its vector. Malvaceous Reservoirs: Okra (*Abelmoschus esculentus*) and various *Hibiscus* species are critical alternative hosts that maintain high viral titers and support whitefly breeding during the off-season (Sattar et al., 2024; Zubair et al., 2024). Weeds: Common weeds such as *Sida* spp. and *Ageratum*

spp. are frequent carriers of both the begomovirus and its associated satellites. Recent studies in 2025 suggest that *Ageratum conyzoides* is a primary site for the recombination of CLCuMuV with other weed-infecting begomoviruses (Biswas et al., 2025). Mixed Farming Systems: The practice of growing vegetables and oilseed crops in close proximity to cotton fields provides a "bridge" for the virus. This continuous availability of hosts provides fertile ground for genetic recombination between different viral strains, leading to the emergence of the highly virulent "Rajasthan" and "Burewala" type variants (Sattar et al., 2024; Iqbal et al., 2025).

Table 5: Correlation Between Meteorological Parameters and CLCuD Incidence

Meteorological Parameter	Correlation with CLCuD Incidence	Impact on B. tabaci
Minimum Temp (Tmin)	Strongly Negative	Lower night temps favor disease.
Maximum Temp (Tmax)	Negative	High heat reduces vector activity.
Morning Humidity (RHm)	Strongly Positive	Increases vector survival and transmission.
Sunshine Hours	Positive	Stimulates whitefly flight and feeding.
Evaporation	Negative	Dry conditions reduce vector build-up.

Statistical modeling using these parameters has achieved high predictive reliability (**R-squared > 0.90**), offering a powerful tool for developing long-term disease forecasting systems (Sain et al., 2025; Sain et al., 2025).

Summary of Findings and Future Perspectives

The complex interplay between the Cotton Leaf Curl Disease (CLCuD) begomovirus complex and its vector, *Bemisia tabaci*, represents one of the most significant challenges to modern cotton agriculture. As documented through the historical trajectory of the disease, the transition from the Multan strain to the resistance-breaking Burewala and Rajasthan strains demonstrates an extraordinary evolutionary plasticity. This genetic flexibility is fueled by high rates of recombination within the monopartite DNA-A genome and its associated satellite molecules (Biswas et al., 2025; Iqbal et al., 2025). The genomic architecture remains a critical focus of study. The virion-sense strand (AV1 and AV2) and the complementary-sense strand (AC1, AC2, AC3, and AC4) coordinate a sophisticated "takeover" of the host plant's cellular machinery. In particular, the AC4 protein and the betasatellite-encoded beta C1 protein serve as the primary suppressors of the plant's innate immune responses, specifically targeting RNA interference (RNAi) pathways (Shafiq et al., 2024; Zhang et al., 2026). From an entomological perspective, the dominance of the Asia II 1 cryptic species in the Indian subcontinent has changed the epidemiological landscape. Its superior vector competency is linked to specialized protein interactions within the whitefly midgut and the protective role of GroEL chaperones produced by endosymbionts like *Arsenophonus*. This allows the virus to survive the insect's immune system and reach the primary salivary glands for persistent transmission (Singh et al., 2024; Wei et al., 2024). Furthermore, environmental epidemiology remains a vital tool for prediction. Current research confirms that morning relative humidity and minimum temperatures are the strongest predictors of disease outbreaks (Sain et al., 2025; Ripamonti et al., 2025). The formula for predicting disease incidence (Y) can be expressed as:

Y = -12.913 (Tmax) + 2.489 (Tmin) + 0.242 (RHm) - 0.197 (RHe) - 0.890 (Rf) + 459.368
(Where T is temperature, RH is relative humidity, and Rf is rainfall).

Looking forward, the integration of traditional management such as optimal sowing dates and the use of modern neonicotinoids like Flonicamid must be combined with biotechnological advancements. The emergence of CRISPR-Cas9 as a tool to directly target the viral nonanucleotide sequence (TAATATTAC) offers a promising path toward permanent resistance (Binyameen et al., 2025; Mubarik et al., 2021).

Table 6: Biological Control Agents and Their Efficacy Against *Bemisia tabaci*

Biological Agent Type	Specific Example	Target Lifecycle Stage	Observed Effect
Parasitoid	*Encarsia formosa*	Nymphs	High parasitization rate; 15-fold increase in control.
Predator	*Chrysoperla carnea*	Eggs and Nymphs	Generalist feeding reduces overall population.
EPF	*Beauveria bassiana*	All Stages	LC50: 2.4 x 10^7 spores/mL on cotton.
EPF	*Aschersonia placenta*	1st-3rd Instar	93–100% mortality in laboratory conditions.

The integration of these biological agents into an Integrated Pest Management (IPM) system helps reduce the reliance on conventional pesticides, which often leads to the development of insecticide resistance in whitefly populations (Zubair et al., 2024; Hassan et al., 2025).

Advanced Biotechnological Interventions: RNAi and CRISPR/Cas

The persistent breakdown of host resistance in conventional cotton varieties has necessitated the development of advanced molecular tools to engineer durable resistance (Mubarik et al., 2021; Ahmad et al., 2024). Two of the most promising technologies are RNA Interference (RNAi) and CRISPR/Cas-mediated genome editing.

RNA Interference (RNAi) Applications

RNAi is a post-transcriptional gene silencing mechanism used to target specific viral genes or the vector itself (Ahmad et al., 2024). By engineering cotton plants to express double-stranded RNA (dsRNA) corresponding to viral sequences, the plant's own cellular machinery is programmed to degrade viral mRNA before translation can occur. Targeted Genes: Successful RNAi constructs, such as the Vb construct, have targeted the AC1 gene (Rep) of CLCuKoV-Bur and the beta C1 gene of the CLCuMuB betasatellite (Ahmad et al., 2024). Recent Advances: Studies in 2024 and 2025 have explored Plant-Mediated RNAi (PM-RNAi), which targets the whitefly vector directly. By expressing artificial microRNAs (amiRNAs) like ghr-miR166b, researchers have developed cotton lines that not only reduce viral accumulation but also significantly lower the survival rates of the feeding *B. tabaci* (Khan et al., 2024). Results: Transgenic cotton plants harboring these constructs have shown remarkable stability across T3 and T4 generations, remaining largely asymptomatic with viral titers 70-80% lower than non-transgenic controls (Khan et al., 2024).

CRISPR/Cas-Mediated Genome Resistance

The CRISPR/Cas system represents a revolutionary tool for directly targeting and cleaving the viral DNA genome (Mubarik et al., 2021). Unlike RNAi, which targets transcripts, CRISPR can target the viral replication origin (the Nonanucleotide sequence) or essential coding regions. Multiplexing Strategy: One of the major challenges with CRISPR is the potential for the virus to "escape" via mutations at the target site. To overcome this, researchers utilize multiplex CRISPR/Cas9 systems that simultaneously target multiple genes, such as AV1 (Coat Protein), AC1

(Rep), and AC2 (TrAP) (Mubarik et al., 2021). Next-Generation Cas Enzymes: As of 2025, the use of LbCas12a has emerged as a superior alternative to Cas9 for CLCuD. Because Cas12a recognizes T-rich protospacer adjacent motifs (PAMs) and creates staggered cuts, it is more effective at disrupting the A-T rich regions found in begomovirus intergenic sequences (Binyameen et al., 2025). Effectiveness: Simultaneous targeting at multiple sites often results in large deletions in the viral genome. In 2025 transient assays using *Nicotiana* and cotton species, multiplex Cas12a constructs achieved up to a 75% reduction in viral accumulation and provided a broad-spectrum defense against multiple strains including CLCuMuV and CLCuKoV (Binyameen et al., 2025; Khan et al., 2024). These biotechnological "add-ons" provide a multi-layered defense essential for a pathogen complex that evolves as rapidly as the CLCuD-associated begomoviruses.

The Third Epidemic and Emerging Strains (2020–2026)

Current field evidence suggests that the Indian subcontinent is in the midst of a third major CLCuD epidemic (Biswas et al., 2025). This new wave is characterized by the resurgence of Multan-like strains and the emergence of highly recombinant variants that threaten the stability of the cotton industry (Shafi et al., 2025; Farooq et al., 2024). Unlike the previous epidemics that were largely restricted by specific ecological zones, the current epidemic is marked by a breakdown of geographical barriers, likely facilitated by the increased movement of the thermotolerant Asia II 1 whitefly cryptic species (Hasan et al., 2025).

Dominance of CLCuMuV-Rajasthan

Since 2018, surveys in the central and southern Punjab regions of Pakistan have identified the *Cotton leaf curl Multan virus-Rajasthan* (CLCuMuV-Raj) as the dominant strain (Zubair et al., 2024). This strain is highly recombinant and is often associated with the *Cotton leaf curl Multan betasatellite-Vehari* (CLCuMuBVeh) (Nawaz et al., 2023). A critical concern is the spread of CLCuMuV-Raj toward the Sindh province, a region that historically harbored different virus species like the *Cotton leaf curl Shahdadpur virus* (CLCuShV) (Khalid et al., 2022). Molecular analysis of isolates from 2020 to 2026 has revealed minor mutations in the C4 and C1 (Rep) genes of CLCuMuV-Raj, indicating that the virus is actively evolving under the pressure of current agricultural practices (Zhang et al., 2026; Zeeshan et al., 2024). These mutations are specifically linked to enhanced suppression of the host's salicylic acid-mediated defense, explaining why previously tolerant cultivars are showing 100% disease incidence in recent Kharif seasons (Basit et al., 2025; Ahmed et al., 2024).

Table 7: Regional Dominance of Begomovirus Strains and Associated Satellites (2020-2024).

Region	Dominant Virus Species (2020–2024)	Associated Satellites	Disease Incidence Observed
Central Punjab (PAK)	CLCuMuV-Raj	CLCuMuB-Veh	High; spreading to Sindh.
South Punjab (PAK)	CLCuMuV-Raj	CLCuMuB-Veh	High; 2-year survey stability.
NW India (Haryana)	CLCuMuV-Raj, CLCuMuV	CLCuMB, GDarSLA	33.6% (2021)
NW India (Punjab)	CLCuMuV-Raj, CLCuKoV-Bur	CLCuMB, CLCuBuA	31–35% (2020–2021)

Recombination and Evolutionary Adaptation

The resurgence of CLCuMuV and its variants demonstrates the failure of the resistance mechanisms developed against the Burewala strain (Sattar et al., 2024; Tahir et al., 2021). Recombination events have been observed in approximately 34% of begomovirus isolates and 40% of satellite sequences collected from *B. tabaci* populations in recent years (Iqbal et al., 2025). This ongoing diversification creates a shifting target for plant breeders and pathologists, necessitating a more proactive and integrative approach to disease monitoring and management (Saleem et al., 2023; Manzoor et al., 2025). Recent transcriptomic profiling suggests that these

recombinants have evolved specific C2 proteins that more effectively counteract host methylation-mediated silencing, a key reason for the rapid breakdown of natural plant immunity (Rehman et al., 2026; Munir et al., 2024).

Conclusion

The whitefly-mediated transmission of cotton leaf curl disease is a paradigm of the complex challenges facing modern agriculture. The interplay between the begomovirus complex, the *B. tabaci* species complex, and the *G. hirsutum* host is a dynamic system shaped by molecular biology, entomology, and environmental epidemiology (Wei et al., 2024; Singh et al., 2024). As the third epidemic continues to unfold, several priority areas for future research and management have been identified:

Precision Vector Monitoring: There is an urgent need for standardized molecular diagnostic tools, such as mtCOI-specific PCR primers, to identify cryptic species like Asia II 1 in real-time (Sain et al., 2025). This monitoring is critical for identifying shifts in vector dominance and proactive detection of insecticide resistance (Zubair et al., 2024; Masood et al., 2022). Field Validation of Biotechnology: RNAi and CRISPR-based resistance particularly the use of LbCas12a must move from glasshouses into large-scale field trials (Binyameen et al., 2025). Recent data suggests that multiplexing gRNAs to target the viral nonanucleotide sequence and the Rep gene simultaneously provides the most durable field-level tolerance (Ahmad et al., 2024; Raza et al., 2025). Climate-Informed AI Management: The integration of deep learning frameworks, such as EfficientNetB3 and Explainable AI (XAI), into disease forecasting allows for 98% accuracy in identifying early-stage infections (Ripamonti et al., 2025). By combining these models with IoT-based humidity and temperature sensors, farmers can take preemptive action up to 14 days before symptoms fully manifest (Sain et al., 2025; Malik et al., 2024). Resistant Cultivar Development: Utilizing genomic insights and Marker-Assisted Selection (MAS) to incorporate broad-spectrum resistance from resilient accessions like Mac-07 into commercial cultivars is essential for long-term stability (Sattar et al., 2024). Current breeding programs in 2026 are focusing on pyramiding these natural resistance genes with transgenic "add-ons" to stay ahead of resistance-breaking strains (Biswas et al., 2025; Tahir et al., 2022). The socio-economic survival of millions of farmers in South Asia depends on the successful management of the CLCuD complex (Faruq et al., 2021). By bridging the gap between molecular pathology and field entomology, the agricultural community can secure the future of global cotton production (Hassan et al., 2024; Saleem et al., 2025).

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