

BREEDING, GENETICS & GENOMICS

A Review of Molecular Hotspots for Whitefly Resistance and Yield in Cotton

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ABSTRACT

***Gossypium hirsutum* L. (upland cotton) is a crucial fiber crop worldwide, yet the whitefly, *Bemisia tabaci* Genn, significantly jeopardizes its production. This phloem-feeding pest causes direct damage to the plant and transmits destructive viral diseases. Sustainable cotton production depends on developing whitefly-resistant varieties exhibiting high yield potential. Fortunately, recent progress in molecular biology and genomics offers promising avenues by enabling the identification of key genetic loci and molecular markers associated with both resistance and yield. Whitefly resistance is crucial for cotton production and a comprehensive understanding of its molecular basis remains essential. This review synthesizes current knowledge on the molecular mechanisms of whitefly resistance in cotton, highlighting key genomic regions and candidate genes linked to both resistance and yield. Finally, it explores the potential of marker-assisted selection and genome editing for developing improved cultivars.**

G*ossypium* species constitute an economically important group of crops, providing natural fiber for the textile industry and seed oil for diverse applications. These products contribute significantly to global economies and the agricultural sector (Sinha et al., 2025). The economic well-being of millions of farmers and agricultural workers worldwide is closely tied to cotton farming, notably in key producing countries such as India, China, U.S., Pakistan, and Brazil (Kaufmann and Tao, 2025). The cotton industry sustains a broad spectrum of economic activities, including textile manufacturing processes (spinning, weaving, dyeing, and printing), garment production, and essential support industries such as the production of textile

machinery, chemical inputs, and transportation services (Haq et al., 2025). Cotton constitutes a significant commodity in international trade, generating substantial revenue for exporting nations and contributing to the maintenance and function of global trade networks (Manzoor et al., 2024). The cotton industry's contribution to employment is substantial, providing livelihoods across its entire value chain, from agricultural production to the manufacturing of finished products, at both national and global levels (Khan and Ali, 2024).

Cotton fiber, valued for its inherent softness and comfort, is ideally suited for clothing and other textile products designed for direct contact with the skin (Nuruzzaman et al., 2024). It serves as a primary source of natural fiber for the textile industry. Cotton's fiber structure allows for air circulation, a property known as breathability, which enhances the comfort of cotton garments in warm weather (Rahaman et al., 2024). The absorbent properties of cotton render it suitable for applications such as towels, bedding, and other absorbent products (Tubcil et al., 2025). In addition, cotton fabrics exhibit relatively high strength and can withstand regular washing and wear (Islam et al., 2024). Cotton's versatility extends from its use in creating a wide range of woven or knitted fabrics with varying textures and properties to the processing of its byproduct, cottonseed, into oil with diverse applications (Vinod et al., 2020). Cottonseed oil is used as a cooking oil, in various food processing applications, and in the production of soaps, cosmetics, and other industrial products. Cottonseed processing yields valuable byproducts such as cottonseed meal that is rich in protein and used as animal feed (Riaz et al., 2023).

Cotton productivity is severely hampered by various biotic and abiotic stresses (Zhang et al., 2025d). These stresses, particularly whitefly (*Bemisia tabaci* Genn) infestation, significantly diminish both the quantity and quality of cotton yields (Fatima et al., 2024). Cotton's growth and development are adversely affected by a range of biotic and abiotic stresses (Patil et al., 2024). Biotic stresses originate from living organisms, whereas abiotic stresses are

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caused by non-living factors (ul Islam et al., 2024). Insect pests, including, but not limited to whiteflies, aphids, bollworms, and thrips pose a significant threat to cotton production (Malinga and Laing, 2024). Damage occurs through various mechanisms, including feeding, disease transmission, and oviposition within plant tissues (Abbas et al., 2025). A range of diseases, caused by fungal, bacterial, and viral pathogens can affect cotton plants leading to various debilitating symptoms, including leaf spots, wilts, and rots (Manzoor et al., 2024). Weed competition for resources such as water, nutrients, and sunlight constitutes significant constraints on cotton yield (Goyal et al., 2025). Abiotic stresses originating from non-living environmental factors represent significant constraints on cotton productivity (Degefu and Gebregiorgis, 2024). These stresses encompass drought, characterized by water deficit; heat stress induced by elevated temperatures; salinity referring to high soil salt concentrations; nutrient deficiencies; and waterlogging resulting from excess water that leads to root oxygen deprivation (Sugumar et al., 2024).

Whiteflies pose a significant threat to cotton production due to the direct damage they inflict. Whitefly-secreted honeydew, a sticky substance, facilitates the growth of sooty mold, which subsequently diminishes photosynthetic activity and compromises cotton fiber quality (Inbar and Gerling, 2008). The escalating resistance of whitefly populations to widely used insecticides complicates effective control and significantly drives up costs. This challenge underscores the urgent need for innovative solutions in pest management (Khalid et al., 2021) and exacerbates the existing threats to cotton production, a crucial source of fiber and oil for the global economy (Abdul Qayyum et al., 2024). Whitefly infestations cause direct damage, transmit yield-limiting viruses, and are becoming increasingly difficult to manage (LaTora et al., 2022). Consequently, research into sustainable control methods, including the development of resistant cotton varieties, is of paramount importance (Maji et al., 2025).

Whiteflies damage cotton plants by feeding on phloem sap, the vascular tissue responsible for transporting sugars and other nutrients from leaves to other plant parts (Belachew and Jenber, 2024). Whiteflies feed by inserting their piercing-sucking stylets into the phloem tissue, the plant's vascular system responsible for transporting sugars and other essential nutrients (Haider et al., 2024). They

then extract this nutrient-rich sap for sustenance. Phloem sap removal by whiteflies depletes essential nutrients, hindering plant growth and development (Singh, 2023). Phloem feeding by whiteflies leads to reduced photosynthesis due to nutrient depletion and transport disruption, further limiting energy production (Sodhi et al., 2025). Simultaneously, the excretion of excess sugars as honeydew coats the leaves. Sooty mold growth on honeydew further reduces photosynthesis by blocking sunlight and impairing plant respiration (Werrie, 2022).

The cumulative effects of nutrient depletion, reduced photosynthesis, and sooty mold growth ultimately lead to yield loss and a reduction in cotton fiber quality (Öztürk et al., 2025). Cotton yield loss, representing a decrease in the total amount of cotton harvested, can be attributed to several factors, including a reduction in the number of bolls, smaller boll size, and a decrease in the weight of cotton fiber obtained per boll (Zhangjin et al., 2025). Cotton fiber quality reduction, a decrease in the desirable properties of the fiber, can have significant economic consequences (Zhang et al., 2025a). This reduction is characterized by shorter fiber length, weaker fiber strength, and contamination with honeydew and sooty mold, ultimately affecting fiber color, dye uptake, and other key processing parameters (Sood et al., 2024). This combined impact makes whiteflies a particularly serious pest (Nadeem et al., 2024).

The widespread use of insecticides results in environmental pollution with detrimental consequences (Majeed et al., 2025). Contamination occurs through air drift, water runoff (affecting rivers, lakes, and groundwater), and soil accumulation, which can negatively impact soil organisms and ecosystem health (Gul et al., 2025). Insecticide use can harm non-target organisms, including beneficial insects, birds, fish, and other wildlife, disrupting the ecosystem (Kumar et al., 2025a). Residues on cotton fibers and potentially in cottonseed products also raise concerns about food safety and human health (Venugopal et al., 2025). Insecticide resistance in whiteflies arises through natural selection. Repeated exposure to an insecticide acts as selective pressure, eliminating susceptible individuals while favoring the survival and reproduction of resistant individuals (Nagaraj et al., 2024). Consequently, the proportion of resistant whiteflies in the population increases over time. The spread of insecticide resistance reduces effectiveness, necessitating higher doses or more frequent applications, thus exacerbating environmental and economic

problems (Junqueira et al., 2024). Cross-resistance can develop, where whiteflies resistant to one insecticide exhibit resistance to others with similar modes of action, limiting control options (Liu et al., 2025b).

Natural biological control of whiteflies is exerted by various beneficial insects, including, but not limited to, ladybugs, lacewings, and parasitic wasps that prey upon or parasitize these pests (Liu et al., 2025c). Broad-spectrum insecticides can disrupt natural whitefly control by killing beneficial insects, potentially leading to pest resurgence and secondary pest outbreaks (Singh et al., 2024c). These concerns necessitate the development of more sustainable and integrated pest management (IPM) strategies that reduce reliance on chemical insecticides (Reay-Jones et al., 2025). IPM emphasizes a combination of methods, including cultural practices (e.g., crop rotation, sanitation, and optimized planting schedules), biological control (use of natural enemies such as beneficial insects and microbial agents), host plant resistance (development of resistant cotton varieties), and when deemed necessary, the application of selective insecticides with more targeted activity and reduced environmental impact (Angon et al., 2023).

Implementing IPM strategies minimizes the negative impacts of pest control on the environment, human health, and long-term sustainability of cotton production by reducing reliance on chemical insecticides (Ke et al., 2025). Resistant cotton varieties possess natural defense mechanisms that deter whiteflies or reduce their ability to thrive, lessening the need for chemical interventions (Kumar and Khurana, 2024). This results in several environmental benefits, including reduced pollution, protection of beneficial insects and wildlife, and minimized risk of insecticide residues (Kumar et al., 2024a). Host plant resistance offers sustainable pest management by providing a durable form of protection, reducing input costs (insecticides, equipment, and labor), and promoting stable cotton yields (Biswakarma et al., 2024).

ENVIRONMENT-FRIENDLY APPROACH

Embracing the power of natural plant defense mechanisms by cultivating resistant varieties aligns with the essential principles of ecology (Badiyal et al., 2024). Reduced reliance on insecticides fosters biodiversity conservation and supports the maintenance of healthy, balanced ecosystems (Mallick et al., 2025). This approach fosters the implementation

of more sustainable agricultural practices aimed at minimizing environmental impact. Cotton varieties exhibit whitefly resistance through various mechanisms. Whitefly resistance in cotton can be conferred by various physical traits (trichomes, leaf structure) and biochemical traits (repellents, anti-feedants, toxins) (Kumaraswamy et al., 2025; Sabra et al., 2025). Developing resistant cotton varieties involves identifying resistance sources (screening varieties and wild relatives) and incorporating resistance genes through breeding or genetic engineering (Ayiecho and Nyabundi, 2025). Developing resistant varieties present challenges, including the potential for whitefly-resistance evolution, necessitating ongoing research and monitoring as well as the need to combine resistance with other desirable traits such as high yield and fiber quality (Bhattarai et al., 2025).

Although resistant varieties are a crucial step toward sustainable cotton production, an IPM approach combining multiple strategies is recommended for optimal and sustainable pest control (Biswakarma et al., 2024). The whitefly has a rapid life cycle (egg, nymph, adult) and high reproductive rate, contributing to its pest status and the development of insecticide resistance (Shafi et al., 2025). Cotton leaf curl virus is not a single viral entity but a complex of begomoviruses, whose spread is influenced by environmental factors and movement of infected plant material (Makeshkumar et al., 2021). Insecticide resistance in whiteflies develops through various mechanisms, including metabolic resistance (increased enzyme production to break down insecticides), target site modification (changes in the insecticide's molecular target), and behavioral resistance (altered insect behavior to reduce exposure) (Nagaraj et al., 2024).

IPM tactics include cultural practices (e.g., crop rotation with non-host crops, crop residue removal), biological control (e.g., chalcidoid wasp [*Encarsia formosa* Gahan] release, lacewing introduction), host plant resistance (using resistant varieties), and selective insecticide use (Anushi et al., 2024). Selective insecticide use in IPM includes insect growth regulators and target-specific insecticides with minimal impact on beneficial insects (Safeena Majeed et al., 2025). Host plant resistance breeding employs techniques such as conventional breeding (crossing resistant and susceptible varieties) (Rai and Rai, 2025), using marker-assisted selection (MAS) to accelerate the process by using DNA markers linked to resistance genes, and genetic engineering

to introduce resistance genes from other organisms (Limenie, 2025). Resistance can deteriorate due to evolving biotypes or strains, necessitating continuous monitoring and development of new resistance sources (Egan et al., 2024). Breeders must simultaneously select for multiple genes, a process that requires sophisticated breeding strategies (Bhuiyan et al., 2025). Breeding strategies for whitefly resistance include conventional breeding, which involves crossing resistant and susceptible varieties and selecting for multiple resistant traits (Yerasu et al., 2025).

Whiteflies, like many insects, can develop insecticide resistance due to evolutionary pressure (Hanuka and Scharf, 2025). Repeated exposure to the same insecticide selects for resistant individuals, who reproduce and pass on resistance genes to their offspring (Ngongang-Yipmo et al., 2025). Over generations, the proportion of resistant whiteflies reduces insecticide effectiveness (Hussein et al., 2025). This resistance arises through various mechanisms, including metabolic resistance (increased enzyme production), target site modification, and behavioral resistance (Lin et al., 2025). The spread of insecticide resistance reduces effectiveness, requiring higher doses or more frequent applications, exacerbating environmental and economic problems (Singh et al., 2024a). Furthermore, cross-resistance can develop, limiting control options as whiteflies resistant to one insecticide can be resistant to others with similar modes of action (Liang et al., 2025).

MOLECULAR MECHANISMS OF WHITEFLY RESISTANCE IN COTTON

The inheritance of whitefly resistance in cotton is complex, being a polygenic trait (Ayiecho and Nyabundi, 2025). In contrast to traits governed by a single gene, whitefly resistance is controlled by numerous genes, each of which contributes incrementally to the overall resistant phenotypes (Brabham et al., 2025). The quantitative nature of whitefly resistance implies that it is not a discrete binary trait. Rather, it exists as a continuous variable, with a spectrum of resistance levels ranging from high susceptibility to high resistance, encompassing numerous intermediate phenotypes (Ravensbergen, 2024). The complex, polygenic nature of whitefly resistance makes breeding for this trait challenging, requiring complex strategies and extensive field evaluations to track multiple genes simultaneously (Farhan Yousaf et al., 2025).

The expression of resistance genes in cotton is subject to modulation by various environmental factors, including, but not limited to, temperature, humidity, plant nutritional status, and the presence of other pests or diseases (Sheri et al., 2025). Variable resistance, where a cotton variety exhibits varying levels of resistance across environments, complicates the development of consistently resistant varieties for diverse growing regions and seasons (Ogwu et al., 2025). Evaluating whitefly resistance in cotton requires rigorous methodologies (Kim et al., 2025). This can involve meticulous control of environmental conditions in controlled environments or implementing multi-location trials to account for the inherent variability of environmental factors (Singh et al., 2024b).

Various mechanisms contribute to whitefly resistance in cotton, including physical traits such as trichomes (leaf hairs) and leaf structure (Kaur et al., 2024). Pest populations are influenced by the quantity of hairs on cotton leaves. There are more whiteflies but fewer leafhoppers when there are more hairs. Butler et al. (1991) reported the number of whiteflies increased significantly at the end of season even with a medium amount of hair present on cotton leaves. Whiteflies were more prevalent on cotton plants with more hairs on the veins of their leaves. However, Zia et al. (2011) reported that plants with longer hairs or thicker leaves had fewer whiteflies. The number of hairs is a major factor for whitefly infestation. Some cotton types naturally fend off whiteflies. However, a plant's outward appearance does not tell the whole story. Adult whiteflies prefer laying eggs on hairy, deep green leaves. Surprisingly, these traits (hairiness and leaf color) do not help the pests in the long run. do Prado et al. (2016) found that even though these plants looked inviting, the whiteflies did not grow faster or live longer. This shows that a leaf might look like a great home on the surface, but the plant's inner defenses can be detrimental to the insect. Whiteflies infest hairy-leaf cotton more than smooth-leaf cotton. Smooth varieties pose the least risk and extremely hairy varieties pose the greatest risk. Culpepper et al. (2024) recommended planting a smooth-leaf cotton variety to reduce the risk of whitefly infestation if planting late or close to other infested fields.

Whitefly resistance in cotton also involves biochemical traits (repellents, anti-feedants, toxins) and often is due to the combined effects of multiple mechanisms (e.g., high trichome density and repellent compound production) (Kumaraswamy et al.,

2025). Because different genes control each of the various resistance mechanisms, breeding for whitefly resistance is complex (Li et al., 2025a). Breeding for whitefly resistance uses MAS and genetic engineering (Sohi et al., 2025). MAS employs DNA markers linked to resistance genes for efficient selection, whereas genetic engineering introduces resistance genes from other organisms for efficient selection (Pandey et al., 2025).

The complex, polygenic, and environmentally influenced nature of whitefly resistance in cotton presents significant challenges to developing durable, resistant varieties (Kumar et al., 2024b). These challenges can be overcome effectively through innovative breeding strategies combined with IPM techniques. This approach not only enhances resilience but also promotes sustainable agricultural practices (Morales-Rodríguez et al., 2025). Integrating resistant varieties into a comprehensive IPM strategy that combines multiple control tactics, is crucial for delaying resistance development and achieving sustainable pest control (Mawcha et al., 2025). By understanding the complexities of whitefly resistance and employing appropriate breeding and IPM strategies, cotton breeders can make significant strides in managing this important pest (Ye et al., 2025).

ANTIXENOSIS (NON-PREFERENCE) DETERING THE PEST

Antixenosis refers to plant traits that deter insect pests from colonizing, feeding, and oviposition, effectively making the plant unsuitable for the pest (Kogan and Ortman, 1978). Several plant traits contribute to whitefly antixenosis in cotton, including leaf surface characteristics such as trichomes, which can physically impede landing and movement, interfere with stylet insertion, and create an unfavorable microclimate (Butter and Dhawan, 2021). Research also has shown hairy-leaf cottons to be more susceptible to silverleaf whitefly compared with smooth-leaf cottons (da Silva Oliveira et al., 2021). Conversely, extremely smooth leaves can deter whiteflies due to difficulty gripping the surface (Morales-Ramos et al., 2023). Leaf color also can influence attractiveness and some studies suggest whiteflies prefer certain shades of green or yellow (Paris et al., 2024). Plants release a variety of volatile organic compounds (VOCs), some of which act as repellents, deterring whiteflies from approaching or settling (Kumaraswamy et al., 2024). Other VOCs

are less attractive to whiteflies or have a masking effect, making the plant less detectable (Gunalan et al., 2024).

Antixenosis plays a crucial role in IPM by naturally reducing pest pressure without direct insect mortality (Chandraleka et al., 2025). This mechanism offers durable resistance, minimizing the risk of rapid resistance development compared to insecticides (Deng et al., 2025). Furthermore, integrating antixenosis with other resistance mechanisms, such as antibiosis and tolerance, enhances pest control efficacy and sustainability (Saini et al., 2025). Exploring antixenosis in cotton breeding enables the development of fewer whitefly-attractive varieties, thereby reducing reliance on chemical interventions and fostering environmentally sound cotton production (Douglas, 2018).

ANTIBIOSIS

Antibiosis, a plant defense mechanism, negatively impacts insect pest biology following initiation of feeding or colonization (Aravinthraju et al., 2024). This can manifest as reduced survival, encompassing increased whitefly mortality across various life stages (egg, nymph, adult), and/or reduced fecundity, resulting in decreased egg production by female whiteflies (Man, 2024). Antibiosis in plants also can hinder whitefly development, prolonging nymphal stages and potentially increasing vulnerability to natural enemies or environmental stressors (Chen et al., 2025). Essentially, the plant exerts a detrimental effect on the pest.

Several key plant factors contribute to antibiosis against whiteflies in cotton (Kumar et al., 2025b). Plants can synthesize toxic secondary metabolites that, upon ingestion, negatively impact whiteflies (Dias and D'Auria, 2025). These compounds can disrupt digestion, metabolism, nervous system function, or other physiological processes, and can act as direct toxins leading to mortality (Abd-Elsalam et al., 2025). Imbalanced plant nutrient composition can induce nutritional stress in whiteflies, negatively impacting growth and development (Jiang et al., 2025b). This can result in reduced survival and fecundity, delayed development, and smaller adult size (Wintraube et al., 2025). Whitefly infestation can induce plant defense responses, leading to the production of deterrent compounds or physiological modifications that reduce plant suitability for the pest (Li et al., 2025c). These induced responses can

include increased synthesis of toxic compounds, alterations in leaf texture or thickness, and activation of systemic signaling pathways (Martín-Cardoso and San Segundo, 2025).

Antibiosis is a valuable IPM component due to its direct impact on pest populations by reducing survival and reproduction (Haider et al., 2025). Although offering relatively durable resistance, the potential for pests to evolve detoxification or tolerance mechanisms exists (Dar et al., 2024). Integrating antibiosis with other resistance mechanisms, such as antixenosis and tolerance, provides more comprehensive and sustainable pest control (Pamidi et al., 2025). Using antibiosis in cotton breeding enables the development of varieties that are both less attractive and directly harmful to whiteflies, further minimizing reliance on chemical interventions (Alia, 2024).

PLANT TOLERANCE

Plant tolerance describes the ability to withstand insect infestation without substantial yield or quality reduction, despite pest resistance and feeding (Sunidhi et al., 2025). Distinct from antixenosis (deterrence) and antibiosis (harm), tolerance emphasizes the plant's capacity to endure pest-induced damage without significant negative impact (Zhang et al., 2025b). Several mechanisms contribute to whitefly tolerance in cotton. Enhanced photosynthetic capacity, for example, allows tolerant plants to compensate for whitefly-induced damage to leaf tissues and maintain adequate photosynthetic rates for growth and development, despite disruption caused by feeding (Vänninen, 2022). Efficient nutrient utilization in tolerant cotton plants allows them to maintain growth and yield despite nutrient depletion caused by whitefly feeding (Dharshini et al., 2025). Furthermore, although tolerance is not directly pest-deterrent or harmful, tolerant plants can activate defense pathways, including rapid tissue repair, antioxidant production to mitigate oxidative stress, and resource reallocation to prioritize growth and reproduction under whitefly stress (De la Riva et al., 2024).

Tolerance is a valuable IPM component as it allows for stable yield despite pest presence (Lenné and Wood, 2024). It also offers durable resistance due to the lack of direct selection pressure for pest-resistance evolution (Brown and Reisig, 2025). Integrating tolerance with antixenosis and antibiosis

enhances pest control robustness and sustainability (Deegala et al., 2025). Using tolerance in breeding enables the development of cotton varieties that maintain productivity under whitefly pressure, contributing to a more sustainable and resilient production system (Meena et al., 2025).

MOLECULAR MARKERS ASSOCIATED WITH WHITEFLY RESISTANCE AND YIELD TRAITS

The development of molecular markers, including random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphism (AFLPs), simple sequence repeats (SSRs), and single nucleotide polymorphisms (SNPs), have revolutionized plant breeding, providing powerful tools for accelerated crop improvement (Kumar et al., 2025c). Molecular markers are specific DNA sequences exhibiting inter-individual variation (polymorphism) within a species, enabling genotypic differentiation independent of phenotypic expression (Miryeganeh and Armitage, 2025). RAPDs employ short, random primers for DNA fragment amplification, generating unique banding patterns (Al-Jayid and Altameme, 2025). AFLPs integrate RFLP and polymerase chain reaction principles to produce numerous polymorphic fragments (Lamichaney et al., 2025). SSRs, or microsatellites, consist of repetitive short DNA sequences with varying repeat numbers, creating polymorphism (Ou et al., 2025). SNPs, the most prevalent variation, represent single base-pair differences in DNA sequence (Wünschiers, 2025).

Using genetic markers to improve complex traits is difficult because many genes are involved. Because markers are not genes, their relationship can deteriorate over time by decreasing precision (Sun et al., 2024b). Every gene has a small impact that is easily overshadowed by other genes or external circumstances (Dixson et al., 2025). Furthermore, every gene influencing a trait does not have a marker and genes frequently interact in intricate ways that are unpredictable (Brault et al., 2025). Lastly, the small gains might not justify the high cost of testing for thousands of markers (Cheng and Luo, 2025).

THE REVOLUTION IN PLANT BREEDING

Molecular markers have revolutionized plant breeding through several key advancements. MAS

enables breeders to directly select target traits, even if phenotypically obscure, by identifying linked molecular markers, thus increasing selection efficiency and accuracy (Kumar et al., 2024c). Molecular markers facilitate genetic mapping, revealing gene location on a chromosome and providing crucial information for understanding complex trait genetics and identifying genes controlling important characteristics (Khakshoor et al., 2025). They also enable germplasm characterization, assessing genetic diversity within and between populations to identify valuable genetic resources (Bokaei et al., 2025). Molecular markers facilitate accurate variety identification, crucial for seed purity and intellectual property protection (Keshavulu, 2025). Furthermore, they enable gene pyramiding, allowing breeders to combine multiple desirable trait genes into a single variety for enhanced crop performance (Chaudhary et al., 2024).

Molecular markers have revolutionized plant breeding by providing powerful tools for efficient selection, genetic mapping, germplasm characterization, variety identification, and gene pyramiding (Garcia-Oliveira et al., 2025). These technologies have accelerated the development of improved crop varieties with enhanced yield, quality, and pest/disease resistance (Istiandari and Faizal, 2025). Critically, these markers have enabled the identification of quantitative trait loci (QTLs) associated with key traits such as whitefly resistance and yield in cotton, highlighting a crucial application in modern plant breeding (Pathak and Yadav, 2025).

QUANTITATIVE TRAIT LOCI

QTLs are genomic regions associated with variation in quantitative traits, which, unlike qualitative traits, are influenced by multiple genes and environmental factors (Bashir et al., 2025). QTLs in cotton include yield, fiber quality, and pest/disease resistance (Bibi et al., 2024). QTL identification is crucial for understanding the genetic architecture of complex traits and developing improved cultivars (Hayat et al., 2025). QTL mapping involves creating a genetic map of the cotton genome using molecular markers to establish a framework for gene and QTL localization (Khan et al., 2025). A diverse population is generated (e.g., via crossing), genotyped using molecular markers, and phenotyped for target traits (Yin et al., 2025). Statistical analysis then identifies QTLs associated with trait variation (Subramani

et al., 2025). Following QTL identification, linked molecular markers enable MAS, facilitating selection based on genotype rather than potentially confounding phenotype (Ayiecho and Nyabundi, 2025). MAS accelerates breeding and enhances selection efficiency for complex traits (Vieira et al., 2025).

Whiteflies significantly threaten cotton yields (Kedar et al., 2025). Molecular markers have enabled the identification of whitefly-resistance QTLs, facilitating the development of more resistant cotton varieties (Sai Timmarao et al., 2025). Yield, a complex trait, is influenced by numerous factors such as plant height, branching, flowering time, and boll size (El-Beltagi et al., 2025). Molecular markers have facilitated the identification of QTLs associated with these yield and morphological traits, enabling the development of higher-yielding cotton varieties (Finnegan et al., 2025). Molecular markers have revolutionized plant breeding by enabling QTL identification and use, leading to the development of cotton varieties with improved pest/disease resistance and higher yields (Boopathi and Shobhana, 2024).

Continued advancements in cotton genomics and genetic data analysis promise further breakthroughs (Luo et al., 2025). Numerous studies have mapped whitefly-resistance QTLs to various cotton chromosomes, identifying candidate genes within these regions, including those involved in defense response pathways (Sun et al., 2024a), cell wall modifications (Wang et al., 2024a), hormonal signaling (Zhang et al., 2022), VOC production (Johnston et al., 2022), detoxification and antioxidant mechanisms (Asghar et al., 2025), proteinase inhibitors (Darweesh et al., 2025), trichome development (Alagarsamy et al., 2024), RNA interference pathways (Karthik et al., 2023), nutrient allocation (Chen et al., 2024b), receptor-like kinases, and resistance genes (Wang et al., 2024b). This highlights significant progress in understanding the genetic basis of whitefly resistance in cotton (Li et al., 2023).

Whitefly resistance in cotton is a complex trait governed by multiple genes, as evidenced by the identification of numerous QTLs distributed across different chromosomes (Nadeem et al., 2024). Several candidate genes, likely contributing to resistance, have been identified within these whitefly-resistance QTLs (Nye et al., 2023). Although specific candidate genes vary across studies and cotton varieties, they often fall into common categories, including receptor-like kinases, resistance genes, genes involved in jasmonic acid and salicylic acid pathways, genes

encoding secondary metabolites, genes involved in RNA interference pathways, genes encoding detoxification enzymes, genes involved in cell wall reinforcement, genes encoding protease inhibitors, genes involved in nutrient allocation, transcription factors, genes encoding pathogenesis-related proteins, genes involved in Redox hemostasis, genes encoding lectins, and genes involved in VOC production (Abd-Elsalam and Hashem, 2025).

Plant defense genes implicated in whitefly resistance include resistance genes, encoding proteins that recognize whitefly-derived molecules and trigger defense responses, and pathogenesis-related proteins, involved in diverse defense mechanisms such as cell wall strengthening, antimicrobial compound production, and systemic acquired-resistance activation (Li et al., 2023). Genes involved in plant-insect interactions also contribute to whitefly resistance (Han et al., 2025a). These include genes regulating trichome development (trichomes can physically deter or trap whiteflies in some reports and trichomes have no or minimal effect on whiteflies in other reports) and genes involved in secondary metabolite production (e.g., terpenoids, alkaloids) that repel or poison the insects (Al-Khayri et al., 2023). Further contributing to whitefly resistance are genes involved in plant signaling pathways, regulating responses to insect attack (e.g., defense hormone production), and genes influencing plant physiology (Roychowdhury et al., 2025) (Table 1). These include genes related to nutrient uptake and transport, which can affect susceptibility to whitefly feeding, and genes involved in plant growth and development, where vigor and health can influence pest resistance (Davis and Thompson, 2024).

GENES USED FOR IMPROVEMENT OF CROPS

Tomato plants with the Mi-1 gene are resistant to whiteflies. It works by causing major changes in the process of gene activation. Numerous internal signaling systems are activated by this process. Certain proteins that function as master switches are subsequently activated by these signals. Finally, these switches activate the defense system of plants. This results in a stronger cell wall and the production of compounds that resist whiteflies (Pascual et al., 2025). A new defense mechanism has been discovered for wild tomato plants. The variety known as LA1840 deters normal growth of whitefly nymphs.

Normally wild tomatoes have sticky hairs on the surface to keep pests away. But this plant fights from the inside out. It uses riboflavin (Vitamin B2) against nymphs either by activating the defense system of the plant or directly damaging the internal system of nymph by creating oxidative stress. It is mainly controlled by the internal vascular system, especially the phloem (Denkers et al., 2025). Transgenic cotton has been developed using a garlic gene, ASAL, that causes cotton to become highly resistant to aphids and whiteflies. The mortality rate of insects feeding on this transgenic cotton is 74% (Najeebullah et al., 2025).

SIGNIFICANCE OF IDENTIFYING CANDIDATE GENES

Identifying whitefly-resistance genes elucidates the underlying molecular mechanisms (Huang et al., 2025). The linked molecular markers derived from these candidate genes can be used in MAS to accelerate breeding for resistant cotton varieties (Hosamani et al., 2025). Gene editing technologies, such as CRISPR-Cas9, offer the potential to modify candidate genes, enhancing existing whitefly resistance or introducing novel resistance genes into cotton cultivars (Verma et al., 2023). Plant defense pathways involve diverse gene categories crucial for resisting pathogens such as whiteflies (Hu et al., 2025). These include plant defense pathways that use gene encoding enzymes involved in phytoalexin biosynthesis (Simas et al., 2025). Phytoalexins are antimicrobial compounds synthesized by plants upon pathogen infection, providing a chemical defense barrier against pathogen growth and development (Pretorius et al., 2025). Phytoalexin composition is species specific (Sun et al., 2025b). Plant defense mechanisms involve multifaceted strategies, including cell wall reinforcement, signal transduction, and the activation of the phenyl propanoid pathway (Fang et al., 2025). Specifically, certain pathogenesis-related proteins enhance cell wall integrity, impeding pathogen penetration, whereas others mediate signal transduction cascades to amplify downstream defense responses (Shelake et al., 2024). Furthermore, the phenylpropanoid pathways, regulated by specific gene expression, yield diverse defense compounds such as lignin, flavonoids, and phytoalexins, thereby contributing to robust plant immunity (Rabeh et al., 2025).

Table 1. Characterization of plant genes contributing to whitefly resistance. Selected plant genes associated with resistance to whiteflies and related pests. Plant species: the plant from which gene was isolated. Gene name: the name of the gene. Gene function/mechanism: the function of the gene and how it relates to pest resistance. Reference: the publication where the gene was first described. TYLCV=Tomato Yellow Leaf Curl Virus, Bt= Bacillus thuringiensis, QTL= Quantitative trait loci, CC-NBS-LRR = Coiled-coil, nucleotide-binding site, Leucine-Rich Repeat.

Plant species	Gene Name	Gene Function/Mechanism	Reference
Tomato (<i>Solanum lycopersicum</i>)	<i>Mi-1</i>	Confers resistance to whiteflies (<i>Bemisia tabaci</i>) and nematodes	Rossi et al., 1998
Eggplant (<i>Solanum melongena</i>)	<i>SmARC</i>	Anthocyanin regulatory gene, indirectly reduces whitefly infestation	Doganlar et al., 2002
Cotton (<i>Gossypium hirsutum</i>)	<i>Cry1Ac</i>	Bt gene, provides resistance to whiteflies and other pests	Kranthi et al., 2005
Garlic (<i>Allium sativum</i>)	<i>ASAL</i>	Allium sativum Leaf Lectin	Saha et al., 2016
Tomato (<i>Solanum lycopersicum</i>)	<i>Ty-2</i>	Confers resistance to TYLCV and whiteflies	Hanson, et al., 2006
Tomato (<i>Solanum lycopersicum</i>)	<i>Ty-3</i>	Another TYLCV resistance gene linked to whitefly resistance	Ji et al., 2007
Cowpea (<i>Vigna unguiculata</i>)	<i>WFS1</i>	Whitefly resistance gene identified through QTL mapping	Muchero et al., 2011
Soybean (<i>Glycine max</i>)	<i>Rag1</i>	Provides resistance to aphids and whiteflies	Hill et al., 2012
Soybean (<i>Glycine max</i>)	<i>Rag2</i>	Another gene conferring resistance to aphids and whiteflies	Hill et al., 2012
Tomato (<i>Solanum lycopersicum</i>)	<i>Ty-1</i>	RNA-dependent RNA polymerase gene, provides resistance to tomato yellow leaf curl virus (TYLCV) transmitted by whiteflies	Verlaan et al. 2013
Cucumber (<i>Cucumis sativus</i>)	<i>CC-NBS-LRR</i>	Resistance gene analog associated with whitefly resistance	Wan et al., 2013
Tomato (<i>Solanum galapagense</i>)	<i>Wf-1</i> and <i>Wf-2</i>	Acyl sugars were found responsible for whitefly resistance	Firdaus et al., 2013
<i>Arabidopsis thaliana</i>	<i>AtRLP52</i>	Receptor-like protein, involved in defense against whiteflies	Zhao et al., 2019

Identifying whitefly-resistance QTLs and candidate genes represents a significant advancement toward a sustainable and effective pest management strategy (Bhattacharyya and Bandyopadhyay, 2025). Understanding the genetic basis of resistance enables researchers and breeders to develop cotton varieties with enhanced whitefly tolerance, ultimately increasing yields and reducing dependence on chemical insecticides (Paul et al., 2025). The genes described play critical roles in plant defense against pathogens (Saha et al., 2024). Understanding their function enables the development of strategies to enhance plant pest and disease resistance, including strategies to enhance plant resistance through MAS using linked molecular markers, and genetic engineering to introduce or modify defense genes (Fatemifard et al., 2024). Harnessing plant genetics enables the development of more sustainable and resilient agricultural systems (Şimşek, 2025). Leaf

morphology, particularly leaf shape, is genetically determined (Jiang et al., 2025a). Diverse leaf shapes result from the action of specific genes regulating leaf initiation, growth, and cell division (Long et al., 2025). Key gene families involved include Knotted1-like Homeobox (KNOX) genes that influence shoot apical meristem maintenance and leaf complexity, Cup-shaped Cotyledon (CUC) genes that define leaf margins and lobes, and Asymmetric Leaves1 (AS1) and Asymmetric Leaves2 (AS2) genes that interact with KNOX genes to regulate leaf shape and size. Leaf size varies significantly within and between species and is influenced by both genetic and environmental factors (Byrne et al., 2024). Genes control cell division, expansion, and overall growth rate (De Lepeleire et al., 2025).

Plant hormones, such as auxin and gibberellins, also regulate leaf size, with genes involved in hormone synthesis, transport, and signaling impacting

leaf growth (Yetgin et al., 2025). Trichomes, hair-like plant surface structures varying in shape, size, and density, are developmentally regulated by a complex gene network (Li et al., 2024). These genes encode transcription factors controlling trichome initiation, growth, and differentiation (Chen et al., 2024a). Key gene families involved include MYB transcription factors that are central to activating the trichome development program, basic Helix-Loop-Helix (bHLH) transcription factors that interact with MYB proteins to regulate initiation, and WD40 repeat proteins that also interact with MYB and bHLH proteins (Li et al., 2025b). These genes significantly influence plant appearance (Sun et al., 2025a). Understanding their function provides insights into plant development and diversity, with applications in crop improvement, stress resistance enhancement, and ornamental plant development (Ramakrishnan et al., 2025).

STRESS RESPONSE

Stress response introduces key gene categories implicated in plant stress responses, specifically those triggered by environmental challenges. Plants face continuous exposure to diverse environmental toxins, including heavy metals, pesticides, and pollutants (Thakur et al., 2025). Effective detoxification mechanisms are thus crucial for plant survival and growth (Szulińska et al., 2025). These genes encode enzymes that detoxify by catabolizing or modifying toxins into less harmful forms, often via a two-phase process (Malcata, 2024). Cytochrome P450s modifies toxins by frequently adding or removing functional groups (Barreda et al., 2024). Cytochrome P450 is involved in whitefly resistance against thiamethoxam insecticide. It is involved in upregulation of CYP6EM1 gene. The upregulation of this gene results in resistance shown by whitefly and silencing of this gene results in susceptibility of whitefly (Huang et al., 2025).

Glutathione S-transferase conjugates the modified toxins with molecules like glutathione, increasing water solubility and facilitating excretion (Ortega et al., 2025). Whiteflies have developed resistance to the insecticide imidacloprid. The resistance is attained with the help of the enzyme BtGSTz1 that helps breakdown toxins (Zhang et al., 2024). Environmental stressors (e.g., drought, heat, heavy metal exposure) induce reactive oxygen species (ROS) production in plants (Rao and Zheng, 2025). These highly reactive molecules can damage cellular

components, including proteins, lipids, and DNA (Sikder et al., 2025). The first QTL for whitefly resistance was identified in cassava. It is located on chromosome 8, which regulates more than one third of the plant defense mechanisms (Chr08_6483145) (Bohorquez-Chaux et al., 2025). Plants have evolved sophisticated antioxidant defense systems to mitigate ROS-induced damage (Chandimali et al., 2025). These genes encode ROS-scavenging enzymes, including superoxide dismutase, (converts superoxide radicals to hydrogen peroxide) (Liu et al., 2025a), catalase (breaks down hydrogen peroxide into water and oxygen) (Ahmed et al., 2025), peroxidases (catalyze hydrogen peroxide reduction) (Hsieh et al., 2025), and glutathione S-transferases, which in addition to detoxification, contribute to antioxidant defense by conjugating harmful compounds with glutathione (Nuevo et al., 2025). These genes are critical for plant stress tolerance (Das et al., 2025). Understanding their function enables the development of strategies for improved crop resilience, including genetic engineering (introducing or modifying these genes) and breeding programs (selecting for desirable alleles) (Vamshi et al., 2025).

MARKER-ASSISTED SELECTION

MAS uses molecular markers (specific DNA sequences) linked to target genes or QTLs to indirectly select for desired plant traits (Ayiecho and Nyabundi, 2025). MAS enables breeders to predict the presence of desirable trait-associated alleles by detecting specific markers, even before phenotypic expression (Sun et al., 2024b). MAS facilitates the early selection of superior genotypes at the seedling stage, eliminating the need for plants to reach maturity and phenotypically express the target trait (Rane et al., 2025). This significantly reduces breeding time and resource expenditure (Léandri-Breton et al., 2025).

MAS enhances selection efficiency and accuracy by directly targeting desired alleles, unlike traditional phenotypic selection, which is susceptible to environmental influence and might not accurately reflect a plant's genotype (Angidi et al., 2025). MAS enables the precise selection of specific alleles within a gene or QTL, allowing breeders to fine-tune the genetic composition of resulting cultivars (Bolouri and Dikmen, 2025). MAS reduces the need for extensive, time-consuming field evaluations by enabling pre-field selection based on marker profiles, thus saving time, labor, and resources (Possamai et al., 2024).

MAS allows breeders to concentrate resources on the most promising lines, thereby enhancing overall breeding program efficiency (He et al., 2024).

MAS has revolutionized plant breeding by accelerating improved cultivar development (Ahtisham and Obaid, 2024). Its capacity for early selection and reduced reliance on field evaluation has significantly enhanced the efficiency and precision of breeding programs (Alemu et al., 2024). One hundred and fifty Pakistani cotton varieties were studied to select whitefly resistant varieties. CA-12 and AGC-155 were selected as best varieties with whitefly resistance by using morphological traits and SSR markers (Rahman et al., 2025). Machine learning algorithms were used to develop whitefly resistant populations in cassava by crossing whitefly resistant ECU72 line and COL2246 susceptible line (Perez-Fons et al., 2025).

CRISPR/CAS9: A PRECISION TOOL

CRISPR/Cas9 is a powerful gene-editing tool comprised of Cas9 (a DNA-cutting enzyme) and a guide RNA that directs Cas9 to a specific target DNA sequence (Karim et al., 2025). CRISPR/Cas9 enables precise targeting and modification of specific cotton genes, a level of precision previously unattainable with other genetic engineering techniques (Tuncel et al., 2025; Zhang et al., 2025c). CRISPR/Cas9 has diverse applications in cotton breeding, including enhancing existing resistance genes (which provide defense against pests and diseases) by modifying their regulatory regions to increase expression (Han et al., 2025b; Singh et al., 2025). CRISPR/Cas9 can improve resistance gene function also by introducing activity, specificity-enhancing mutations, and silence susceptibility genes making plants more resistant by inactivating these genes (Ikram et al., 2025; Singh et al., 2025). CRISPR/Cas9 can introduce novel resistance genes into cotton via gene editing (modifying existing genes) or gene insertion (introducing genes from other organisms) (Singh et al., 2025; Weldemichael and Gebremedhn, 2025).

CRISPR/Cas9 contributes to sustainable agriculture by facilitating the development of resilient cotton varieties, thus reducing reliance on chemical inputs like pesticides (Priyatham et al., 2025). CRISPR/Cas9 has the potential to revolutionize cotton breeding by enabling the development of more resilient and sustainable varieties with enhanced pest and disease resistance, improved yield, and superior

fiber quality (Jahan et al., 2025). The development and deployment of genetically modified crops necessitate careful consideration of ethical, environmental, and regulatory implications (Subburayalu et al., 2024). Five hundred and two genes in cotton related to sucking insects (aphids and whitefly) have been modified with a success rate of 97%. Upregulation of the GhMPL423 gene makes cotton more resistant to pests by triggering the natural defense system of plants. This discovery allows breeders to develop cotton that naturally fights insects without needing foreign genes (Sun et al., 2024a). Cotton plants use specific non-coding RNAs (IncA07 and IncD09) as their main defense against sap-sucking insects like whiteflies. By using CRISPR/Cas-9, it was revealed that down regulation of these RNAs greatly increased the susceptibility of plants to infestation. These RNAs control the jasmonic acid hormone pathway (Zhang et al., 2022)

CONCLUSION AND FUTURE PERSPECTIVES

Significant advancements in cotton breeding have been driven by molecular markers and genomic tools, enabling the deciphering of the cotton genome and the identification of key traits such as whitefly resistance and yield (Naeem et al., 2025). Molecular markers, including RFLPs, RAPDs, AFLPs, SSRs, and SNPs, serve as genomic signposts for tracking trait inheritance, whereas genomic tools such as genome sequencing, QTL mapping, and genome-wide association studies provide comprehensive genome analysis (Majhi et al., 2024). QTL mapping identifies genomic regions associated with traits, allowing for the discovery of candidate genes, which are further investigated and manipulated using MAS and genomic editing technologies like CRISPR/Cas9 (Bolouri and Dikmen, 2025). These tools enhance breeding efficiency by enabling precise modifications, such as improving resistance genes, silencing susceptibility genes, and introducing novel resistance traits (Kumar et al., 2024c).

The integration of molecular and conventional breeding methods accelerates the development of superior cotton cultivars with enhanced pest resistance, higher yields, and improved fiber quality, promoting sustainable agriculture by reducing reliance on chemical inputs (Khan et al., 2024). Future research should focus on fine-mapping QTLs to identify causal genes, developing cost-effective,

high-throughput molecular markers, and validating MAS effectiveness across diverse cotton germplasm (Mores et al., 2021). Additionally, exploring CRISPR/Cas9 for enhancing whitefly resistance and yield, while addressing off-target effects and delivery methods, is crucial (Jiang et al., 2025b). Integrating molecular approaches with traditional breeding strategies, such as using molecular data to guide parental selection and progeny evaluation, will further optimize breeding programs (Sharma et al., 2025). Combining multiple resistance genes into single varieties can provide durable solutions to whitefly infestations, whereas molecular tools can identify yield-related QTLs and modify key yield components (Haq et al., 2024). By reducing pesticide reliance and increasing productivity, these advancements contribute to sustainable cotton production and global food security, ultimately benefiting farmers, the textile industry, and environmental sustainability (Dutta and Sinha, 2025).

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