



REVIEW ARTICLE

Breeding and biotechnological strategies for enhancing sucking pest tolerance in cotton: Current perspectives and future prospects

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Abstract

Cotton is often hailed as the "white gold" of agriculture due to its unparalleled contribution to the global textile industry, economic sustainability and rural livelihoods. Cotton possesses natural fibre of high-quality. It supports millions of farmers worldwide and serves as a vital raw material for many industries. However, cotton production is severely threatened by pest attacks. Sucking pests such as aphids (*Aphis gossypii*), whiteflies (*Bemisia tabaci*), thrips (*Thrips tabaci*) and jassids (*Amrasca biguttula biguttula*) affect cotton productivity to a significant extent. These pests not only cause direct damage to the crop by feeding on plant sap but also act as vectors of viral diseases, leading to substantial yield and fibre quality losses. Conventional pest management practices depend on chemical pesticides, which pose environmental risks, increase production costs and lead to pesticide resistance. Breeding for sucking pest tolerance is a sustainable alternative that enhances crop resilience while reducing dependence on chemical control measures. Exploring the genetic basis of sucking pest resistance in cotton, emphasizing key Quantitative Trait Loci (QTLs), resistant genotypes and physiological and morphological defense mechanisms such as trichome density, leaf toughness and secondary metabolites are prerequisite for creating sucking pest tolerance. KC2 and JR 23 are found to be promising jassid resistant varieties developed through conventional breeding in cotton. Advances in molecular breeding, Marker-Assisted Selection (MAS) and genomic tools have enabled more precise identification and incorporation of resistance traits into elite cultivars. Additionally, transgenic and gene-editing approaches have also proven useful in developing pest tolerant varieties retaining the fibre quality and yield. Breeding strategies along with genomic selection, multi-environment testing and biotechnological innovations can be used to develop sucking pest-tolerant cotton varieties suited to diverse agro-climatic conditions. This review highlights the different strategies crucial for improving sucking pest resistance in cotton.

Keywords: biotechnological approaches; breeding approaches; cotton; sucking pest

Introduction

Cotton (*Gossypium* spp.) is one of the most important commercial crops all over the world. It contributes significantly to the global textile industry and support livelihoods of millions of farmers, especially in developing countries (1). Cotton's economic value is not only because of its fibre but also its by-products, such as oil and seeds, which are used in food and feed industries (2). However, cotton production is severely constrained by a range of biotic stresses. Most of the damaging effect to the cotton crop is caused by sucking pests (3). These pests include aphids (*Aphis gossypii*), whiteflies (*Bemisia tabaci*), jassids (*Amrasca biguttula biguttula*), thrips (*Thrips tabaci*) and mealybugs (*Phenacoccus solenopsis*). All these leads to substantial yield losses and degrade fiber quality.

The damage inflicted by sucking pests occurs through their feeding on plant sap, which weakens the cotton plant, causes stunting, reduces photosynthesis and leads to leaf

deformation (4). In addition to direct damage, these pests act as vectors for numerous viral diseases, including Cotton Leaf Curl Virus (CLCuV) and Cotton Mosaic Virus (CMV), which aggravate the crop's decline. The effect of sucking pests is immense resulting in huge crop loss and reduction in yield. This loss is estimated to be billions of dollars annually (3). The conventional approach to manage these pests has mainly relied on the use of chemical pesticides. Though pesticides provide immediate relief but lead to several ecological and economic issues such as pesticide resistance, environmental degradation and harm to non-target organisms. Furthermore, the escalating concerns of pesticide residue in cotton products have prompted a growing demand for sustainable and eco-friendly pest management strategies (5). As a result, interest in development of pest-resistant cotton varieties through breeding has increased. The development of sucking pest-resistant cotton varieties in India has evolved in response to changing pest dynamics, particularly following the introduction of Bt cotton in 2002. In the pre-Bt era,

traditional desi cottons (*Gossypium arboreum* and *G. herbaceum*), known for their inherent tolerance to sucking pests due to traits like leaf hairiness and higher gossypol levels, served as the foundation for early breeding efforts. Varieties such as KC 2, JR 23, Khandwa 2 and SRT-1, developed between the 1980s and early 1990s, were recognized for their moderate resistance to pests like jassids and aphids. These varieties gained popularity among farmers in central and southern India due to their adaptability and lower pesticide requirements.

The introduction of Bt cotton in 2002, while effective against bollworms, inadvertently led to increased incidence of sucking pests such as whiteflies, aphids, jassids and mealybugs, as Bt offered no protection against them. This prompted a strategic shift in breeding programs toward incorporating sucking pest resistance. Public sector institutions developed varieties like PA 255 (2005) and F1861 (2007) with improved jassid tolerance. In the following years, varieties such as Suraj (2015) and PA 812 (2018) were released with broader tolerance to multiple sucking pests.

Recent efforts have included field screening of wild cotton species, such as *Gossypium sylvestre*, leading to the identification of resistant lines like DGS-18, DGS-26 and DGS-28, which are now being used in resistance breeding. Additionally, the integration of MAS and emerging tools such as Genome-Wide Association Studies (GWAS), genomic selection and CRISPR/Cas9-based genome editing, are now enhancing the precision and speed of breeding. These technologies are enabling the development of next-generation cotton varieties with stacked resistance traits, better suited for sustainable, Integrated Pest Management (IPM) strategies and reducing the crop's dependence on chemical insecticides.

Breeding for pest tolerance has emerged as a key strategy in reducing the dependence on chemical pesticides while ensuring sustainable cotton production. By enhancing the plant's natural ability to tolerate pest infestation, Breeding programs prove useful in enhancing plant ability to tolerate pest infections and pest management in an eco-friendly manner (6). Cotton breeding for pest resistance typically involves selecting for traits that either deter pests from feeding or reduce their ability to cause damage (7). Advances in molecular breeding, the identification of pest resistance genes and the use of biotechnological tools have all contributed to the development of pest resistant cotton varieties.

This review aims to summarize the current state of knowledge on breeding and other strategies used for development of sucking pest tolerant varieties of cotton. The major pests affecting

cotton production, the mechanisms by which cotton develops resistance and the approaches used in development of pest-resistant varieties have been discussed in this review. Furthermore, the integration of pest-tolerant varieties into IPM strategies, challenges in development of pest tolerant cotton and future prospects of the development of sustainable, pest-resistant cotton cultivars is also discussed.

Sucking pest in cotton

Sucking pests are a major concern for cotton farmers, as they can significantly affect the health and yield of cotton plants. These pests feed on plant sap, causing direct and indirect damage. This section provides detailed information related to primary sucking pests in cotton including major features of their identification, life cycles, feeding habits and the types of damage they cause to cotton crops.

Aphids (*Aphis gossypii*)

Identification and biology: Aphids are small, soft-bodied insects that are typically green, yellow or black in colour, but can also appear in other colours. They have pear-shaped bodies, long antennae and two tubes (cornicles) extending from the rear end of their bodies. Aphids are known for their rapid reproduction rates and can produce several generations in a single growing season.

Life cycle: Aphids reproduce through both sexual and asexual means, with a predominance of asexual reproduction during the growing season. Female aphids give birth to live young (nymphs), which mature quickly and can begin reproducing in just a few days. Aphids can be found on the undersides of leaves and on young shoots.

Feeding behaviour: Aphids feed by piercing plant cells with their needle-like mouthparts and sucking out plant sap. This feeding can weaken the plant, reduce growth and cause leaves to curl or become distorted. They also secrete a sticky substance called honeydew, which attracts mold and other pests.

Damage caused by aphids:

Direct damage: Aphid feeding depletes plant nutrients and reduces plant vigour, leading to stunted growth and yellowing of leaves (chlorosis). Heavy infestations can result in wilting and defoliation.

Indirect damage: Aphids are vectors for several plant viruses, including the CLCuV, which can cause severe crop loss. The honeydew excretion can also lead to fungal growth, further damaging the plant (Fig. 1).

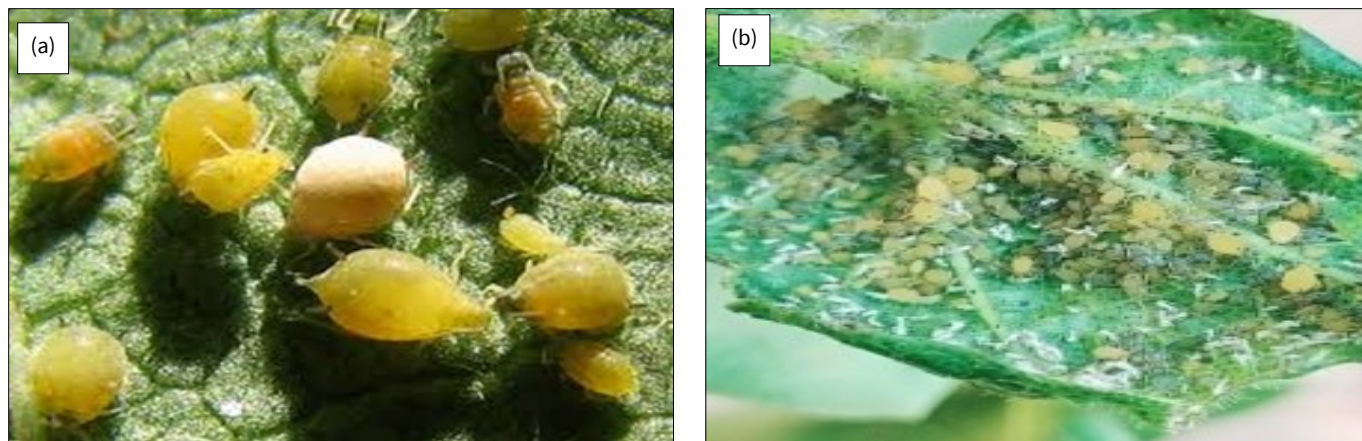


Fig. 1. Aphid infestation and associated leaf damage. a) Aphids; b) Leaf damage caused by aphids

Whiteflies (*Bemisia tabaci*)

Identification and biology: Whiteflies are small, white, moth-like insects. They are characterized by their powdery white wings, which are held in a roof-like position when at rest. Nymphs are flat, oval and yellow or green and they remain on the underside of leaves. Whiteflies are common pests in warm climates and can infest cotton plants during the growing season.

Life cycle: The life cycle of whiteflies includes the egg, nymph (several instars), pupa and adult stages. Whiteflies lay eggs on the undersides of cotton leaves and the nymphs hatch and begin feeding on the plant sap. They undergo several nymphal stages before emerging as adults.

Feeding behaviour: Whiteflies feed by inserting their piercing-sucking mouthparts into plant cells and extracting sap. Like aphids, they secrete honeydew, which can lead to the growth of sooty mold and further reduce photosynthesis in the plant.

Damage caused by whiteflies:

Direct damage: Whiteflies cause wilting, yellowing and stunted growth of cotton plants due to their sap-feeding behaviour. A high population density can severely affect the plant's health, leading to defoliation.

Indirect damage: Whiteflies are also known vectors of plant viruses, including CLCV, similar to aphids. Their feeding behaviour weakens the plant, making it more susceptible to diseases. The honeydew secretion can encourage the growth of sooty mold, which can cover the leaves and further reduce photosynthetic capacity (Fig. 2).

Cotton jassids or leaf hopper (*Amrasca biguttula biguttula*)

Identification and biology: The cotton jassid is a small, wedge-shaped insect with a pale green or yellow body and a distinct black spot on each side of its thorax. Jassids are active pests of cotton in many parts of the world, especially in tropical and subtropical climates.

Life cycle: The jassid has an incomplete metamorphosis cycle, including the egg, nymph (which molts several times) and adult stages. Eggs are laid on the undersides of leaves and the nymphs feed on the plant sap, gradually growing into adults.

Feeding behaviour: Jassids feed by piercing plant cells and sucking out the sap. They are known to target young cotton plants, particularly the tender leaves, stems and squares (flower buds). Jassids are capable of transmitting CLCuV, which can lead to severe yield losses.

Damage caused by jassids:

Direct damage: Feeding by jassids causes chlorosis, leaf curling and stunted growth. The damage is particularly evident in young plants and during the early stages of growth. Severe infestations can cause defoliation and reduce the number of bolls (fruiting bodies) produced by the plant.

Indirect damage: Jassids are vectors of CLCuV, which can cause dramatic reductions in yield and quality. The virus can affect the leaves, cause curling and deformations and ultimately leading to plant death in severe cases (Fig. 3).

Mealy bugs (*Phenacoccus* spp.)

Identification and biology: Mealybugs are small, soft-bodied insects with a waxy, cotton-like appearance. They are typically white or pinkish and have a distinctive appearance due to the waxy coating they produce. Mealybugs are often found on the undersides of leaves, on stems and in the cotton bolls.

Life cycle: Mealybugs go through an egg, nymph and adult stage. The nymphs are the feeding stage and are typically found in clusters on the plant. The adult females remain immobile and can produce hundreds of eggs in a single generation.

Feeding behaviour: Mealybugs feed on plant sap by inserting their needle-like mouthparts into plant tissue. They are typically found in colonies and cause extensive damage by draining the plant's nutrients.

Damage caused by mealybugs:

Direct damage: Mealybug feeding results in a reduction in plant vigour, causing yellowing and wilting of leaves. Heavy infestations can lead to stunted growth and loss of bolls, reducing overall cotton yield.

Indirect damage: Like other sucking pests, mealybugs excrete honeydew, leading to the development of sooty mold. They can also spread plant pathogens, leading to disease outbreaks in cotton fields (Fig. 4).

Other minor sucking pest: thrips (*Frankliniella* spp.)

Thrips are tiny, slender insects that can cause damage to cotton plants by feeding on the young leaves, buds and flowers. They are also vectors for several plant viruses, particularly in the early stages of plant growth. Although they are not as impactful as aphids or whiteflies, they can still contribute to the overall pest pressure in cotton fields.



Fig. 2. Whitefly infestation and associated leaf damage.
a) Whitefly; b) Leaf damage caused by whiteflies



Fig. 3. Jassid infestation and associated leaf damage.
a) Jassids; b) Leaf damage caused by aphids



Fig. 4. Mealybug infestation and associated leaf damage.
a) Mealy bug; b) Leaf damage caused by mealy bug

Identification and biology: Thrips are minute, slender-bodied insects measuring about 1-2 mm in length. They are typically yellow, brown or black in colour and possess narrow, fringed wings. The adult thrips are highly mobile and can fly short distances, while the nymphs are wingless and often appear pale yellow. Thrips are usually found on the undersides of leaves, flower buds and in leaf axils.

Life cycle: Thrips undergo incomplete metamorphosis, progressing through the following stages: egg, nymph, prepupa, pupa and adult. Eggs are inserted into plant tissues by the female using a saw-like ovipositor. Nymphs hatch and begin feeding on plant sap; they undergo two active instars. Prepupal and pupal stages are non-feeding and often occur in soil or leaf litter. Adults emerge and continue feeding and reproducing. A single generation can be completed in 2-3 weeks under favourable conditions, allowing for rapid population increases.

Feeding behaviour: Thrips possess piercing-sucking mouthparts that puncture plant cells to extract sap. Both nymphs and adults feed by rasping the plant surface and sucking out the contents. Feeding is typically concentrated on young leaves, buds, flowers and tender fruit surfaces.

Damage caused by thrips:

Direct damage: Leaves show silvery, bronzing, curling or streaking due to cell destruction. Flowers may become deformed, leading to reduced pollination and fruit set. Damaged fruits or bolls show scarring and discoloration, affecting marketability. Severe infestations may cause stunted growth and leaf drop.

Indirect damage: Thrips excrete honeydew, which may lead to sooty mold development. Certain species, such as *Frankliniella occidentalis*, act as vectors for Tospoviruses, including Tomato Spotted Wilt Virus (TSWV), contributing to further crop losses (Fig. 5).

Approaches for developing sucking pest tolerant cotton plants

Sucking pests, such as aphids, whiteflies, mealy bugs, jassids and thrips can severely reduce yields by direct feeding damage and through the transmission of plant viruses. Development of plants resistant to stress caused by sucking pests in cotton is a critical for getting sustainable cotton production. The development of cotton varieties resistant or tolerant to these pests involves a combination of traditional breeding methods, molecular approaches and modern biotechnological innovations. This section discusses in detail about these approaches and provides a comprehensive understanding of the various strategies for improving resistance to sucking pests in cotton (Fig. 6).

Breeding techniques

Conventional breeding: Conventional breeding techniques can be adapted for inducing pest resistance in plants. The cotton varieties that show natural resistance to sucking pests are selected and crossed. This strategy is adopted by breeders and used for developing high-yielding cultivars that are less susceptible to pest damage.

Natural resistance: Natural resistance to sucking pests is often categorized into three primary mechanisms: non-preference, antibiosis and tolerance (Fig. 7).



Fig. 5. Thrips infestation and associated leaf damage.
a) Thrips; b) Leaf damage by thrips

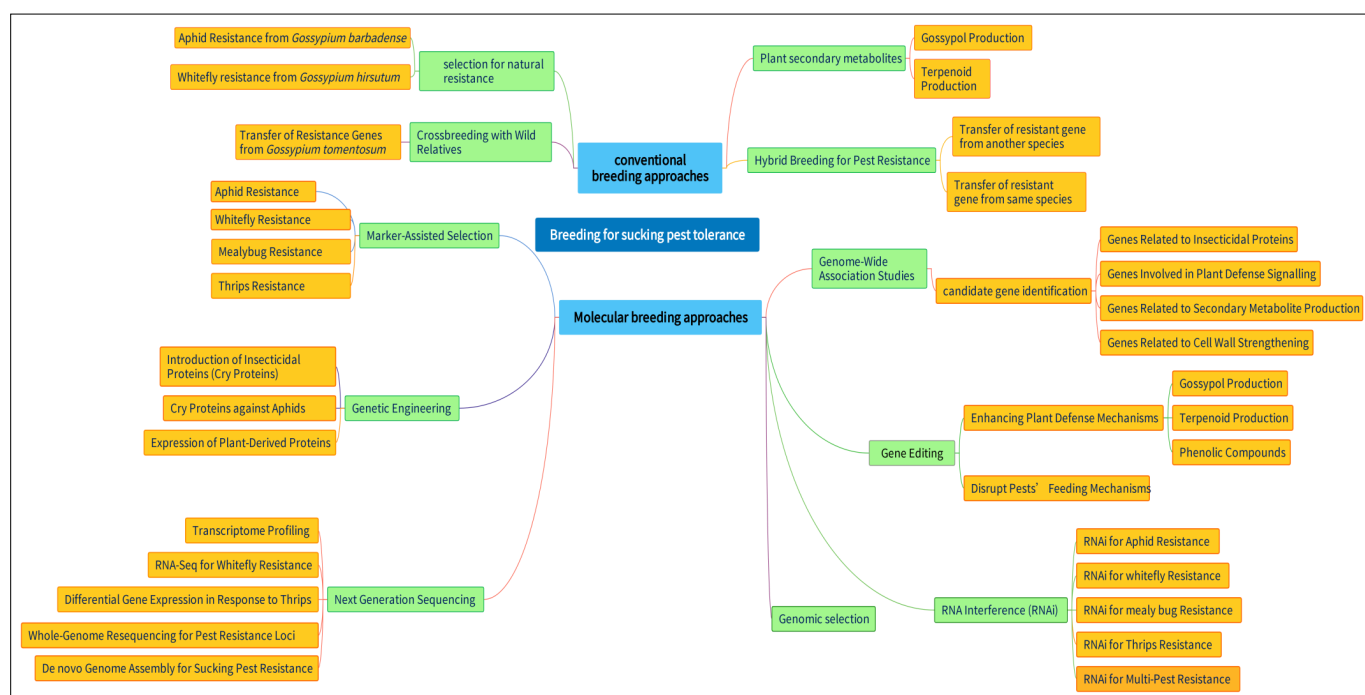


Fig. 6. Natural mechanism of sucking pest tolerance.

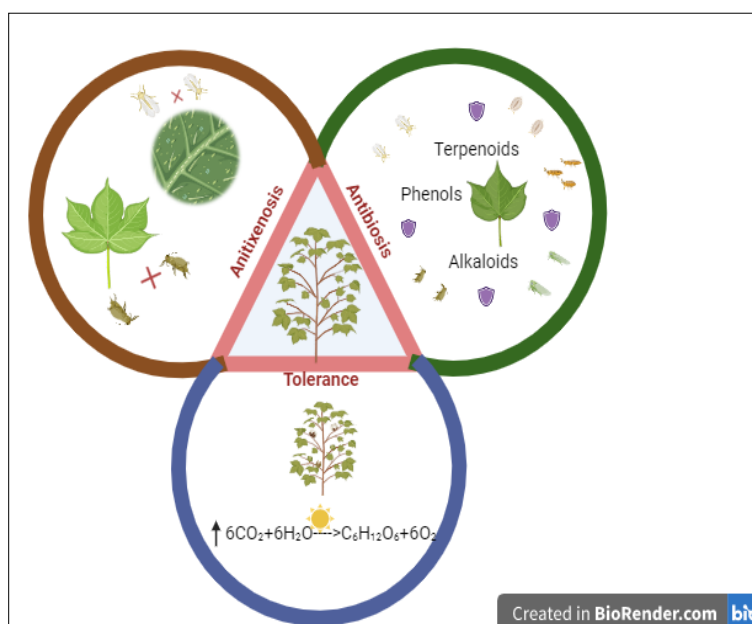


Fig. 7. Approaches for sucking pest tolerance in cotton.

Antixenosis (non-preference): Several cotton varieties exhibit resistance to sucking pests through physical traits such as trichomes (hair-like structures) and waxy cuticles. These structures hinder pest feeding and trap or deter pests, reducing their ability to cause damage. Cotton varieties with a higher density of leaf trichomes can physically deter sucking pests like jassids and whiteflies, making it harder for them to feed and lay eggs. Thicker leaves can be a deterrent for aphids due to the difficulty in penetrating the tissue with their stylets. High densities of glandular and non-glandular trichomes are particularly effective in repelling pests like whiteflies and aphids (8,9).

Antibiosis: Cotton plants produce a range of secondary metabolites such as terpenoids, phenolics and alkaloids, which can deter pest feeding or inhibit pest development. The concentration and composition of these chemicals vary among cotton varieties and can play a pivotal role in the plant's resistance. For instance, cotton varieties with higher levels of gossypol (a toxic compound) or phenolic compounds tend to exhibit greater tolerance to aphid infestation (10).

Tolerance: The resistance mechanisms directly prevent damage caused by the pest while tolerance allows the plant to endure pest attacks without significant yield loss. Tolerant cotton varieties can maintain high productivity despite the presence of pests by compensating for damage, enhancing photosynthetic efficiency or increasing the plant's ability to recover from feeding stress (11-14).

Other specific natural resistance mechanisms include:

Aphid resistance from *Gossypium barbadense*: *Gossypium barbadense*, a cotton species with superior fibre quality, has been studied for its resistance to aphids. Researchers have identified that certain varieties of *G. barbadense* produce compounds like gossypol and terpenoids that inhibit aphid feeding and reproduction. These compounds could be successfully transferred to *Gossypium hirsutum*, the main species used for cotton production (15).

Selection for whitefly resistance in cotton: Several studies have shown that certain cotton varieties naturally exhibit resistance to whiteflies, such as *Gossypium hirsutum* varieties with high levels of gossypol and terpenoids. These varieties have been used in conventional breeding programs to improve whitefly resistance in commercial cotton cultivars (11,16).

Crossbreeding with wild relatives: The wild relatives of cotton species, especially from the *Gossypium* genus, are a valuable source of resistance to sucking pests. These species have evolved resistance mechanisms over time and possess genes that confer resistance to various pests, including aphids, whiteflies and jassids.

Transfer of resistance genes from *Gossypium tomentosum*: *Gossypium tomentosum*, a wild cotton species found in the Pacific Islands, exhibits high levels of resistance to several sucking pests, particularly whiteflies and jassids. Efforts have been made to introgress resistance genes from *G. tomentosum* into cultivated cotton species through hybridization and backcrossing (17,18).

Compared with the commercial *Gossypium hirsutum* L. cv. Sicot 71, thrips were significantly less abundant and imposed markedly less damage on the diploid genotypes *Gossypium arboreum* L. (BM13H, Roseum A256), *Gossypium thurberi* Tod. (GOS5310) and *Gossypium trilobum* (Moc. & Sess. ex DC) Skov. (GOS5332). The mechanism contributing to the resistance of those diploid species could be extensively studied and these

species could be used as donors for introgression of resistance in cultivated varieties (19).

Breeding for tolerance using plant secondary metabolites: Cotton plants naturally produce a range of secondary metabolites, such as gossypol, terpenoids and alkaloids which have pesticidal properties and help in defending against pests. Breeding cotton for enhanced production of these compounds has been a key strategy for improving pest resistance.

Gossypol production and sucking pest resistance: Gossypol is a toxic compound that is found in varying levels in cotton plants, particularly in the glandular tissues which exhibit lethal effect on aphids, whiteflies and jassids. By breeding cotton varieties that produce higher levels of gossypol, breeders can increase the plant's resistance to these pests. Breeding for cotton varieties with higher gossypol content has been shown to reduce aphid infestation levels and increase plant resistance. These varieties exhibit both direct toxicity to aphids and reduced aphid reproduction (20).

Terpenoid production and pest resistance: Terpenoids are another class of secondary metabolites that contribute to cotton's resistance to sucking pests. These compounds, particularly monoterpenes and sesquiterpenes, act as repellents or feeding deterrents for pests. Studies by researchers have shown that cotton plants with high levels of terpenoids tend to have fewer sucking pest infestations. By selecting cotton varieties with enhanced terpenoid production, breeders aim to create varieties that are less attractive to pests and better resistance against pest damage (21-23).

Metabolite-based resistance breeding plays a crucial role in IPM by reducing reliance on chemical insecticides and enhancing the plant's innate defense mechanisms. By selecting for specific secondary metabolites that deter or disrupt sucking pests, it contributes to long-term, environmentally sustainable pest control. This approach also supports compatibility with other IPM components like biological control and cultural practices, leading to more resilient agro ecosystems.

Hybrid breeding for pest resistance: Hybrid breeding involves crossing two or more genetically diverse cotton lines to combine desirable traits such as pest resistance. By crossing cotton lines with varying levels of resistance to different pests, breeders can develop hybrid varieties that exhibit high resistance to a range of sucking pests. Several hybrid cotton varieties have been developed by crossing high-yielding commercial cultivars with pest-resistance. These hybrids exhibit increased resistance to aphids, whiteflies and jassids, along with better overall yield and fibre quality (24,25). Research has successfully introgressed thrips resistance from pima cotton (*Gossypium barbadense*) into upland cotton (*Gossypium hirsutum*) through hybridization and backcrossing. The resistant lines with specific chromosomal introgressions were found to be associated with chromosomes A10 and D11 (26). The identified Introgression Lines (ILs) provide a genetic resource for breeding programs aimed at developing resistant cotton cultivars.

Biotechnological approaches for sucking pest tolerance in cotton: Biotechnological approaches have proved useful in addressing the challenges posed by sucking pests in cotton. By harnessing modern tools such as genetic engineering, RNA interference (RNAi), CRISPR/Cas9 genome editing and molecular markers, researchers and breeders are now able to create cotton varieties with enhanced resistance to sucking pests like aphids, whiteflies,

mealy bugs and thrips. These technologies allow for more precise, sustainable and effective control of pests which is critical in the face of growing pest resistance to chemical pesticides and the environmental concerns associated with pesticide use.

MAS for sucking pest resistance in cotton: MAS has become a basis of modern cotton breeding programs, particularly complex traits such as resistance to sucking pests. The pests including aphids, whiteflies, thrips and mealy bugs, cause significant damage to cotton crops. MAS influence molecular markers that are linked to resistance genes, allowing for more efficient selection and faster development of pest-resistant cotton varieties.

Process of MAS for sucking pest resistance in cotton: The MAS process generally involves the following steps:

Mapping resistance genes/QTLs: The first step in MAS is the identification and mapping of QTLs associated with resistance to sucking pests in cotton. This typically involves generating a genetic linkage map using molecular markers and then identifying the loci that influence pest resistance. QTL mapping requires the use of bi-parental populations (such as F₂ or recombinant inbred lines) derived from resistant and susceptible cotton varieties. Mapping studies have revealed that leaf hopper tolerance was tagged on chromosomes A5 and A11 (27).

Marker discovery: After mapping, the next step is to identify molecular markers that are tightly linked to the resistance loci. These markers can include SSRs, SNPs, RAPDs and AFLPs. Markers are then validated and used for MAS.

Screening and selection: Once the markers are identified, they are used to screen large populations of cotton plants. The plants are selected based on the presence of resistance-linked markers. This allows for early selection and reduces the time and resources needed to evaluate pest resistance in the field.

Backcrossing and development of resistant varieties: Using MAS, the identified resistance genes or QTLs can be transferred into elite cotton varieties via backcrossing. In each backcross generation, the selected plants are screened for the presence of the resistance-linked markers, ensuring the rapid incorporation of resistance traits.

Field testing and validation: Although MAS can accelerate the selection of pest-resistant cotton, field testing is still necessary to validate the resistance in natural environments. The selected plants are grown in pest-infested fields to ensure that the resistance holds under real-world conditions.

MAS for aphid resistance in cotton: Aphids (*Aphis gossypii*) are one of the most problematic sucking pests in cotton farming, causing direct damage by feeding on the phloem and indirectly by transmitting plant viruses. Research on MAS for aphid resistance focuses on identifying QTLs linked to resistance. Resistance to aphids in cotton is typically controlled by multiple genes and several QTLs linked to aphid resistance have been identified in chromosome 17 and 22 (28-30).

MAS for whitefly resistance in cotton: Whiteflies (*Bemisia tabaci*) are notorious for not only damaging cotton plants through sap feeding but also transmitting viruses such as CLCuV, leading to severe yield losses. MAS has been successfully applied to enhance whitefly resistance in cotton by targeting specific QTLs associated with whitefly resistance. Molecular studies have revealed QTLs for whitefly resistance in cotton, including loci on chromosomes 6, 16 and 21 (31,32).

MAS for mealybug resistance in cotton: Mealybugs (*Phenacoccus* spp.) are another major sucking pest of cotton. Their feeding behavior results in yield loss and the secretion of honeydew, which facilitates the growth of sooty mold. The use of MAS to improve mealybug resistance has gained attention in recent years. Several studies indicated that key genetic markers for resistance have been identified. Resistance mechanisms to mealybugs in cotton have been linked to QTLs on chromosomes 9 and 13 (32).

MAS for thrips resistance in cotton: Thrips (*Thrips tabaci*) are important pests in cotton, especially during the seedling stage, causing feeding damage that can stunt plant growth. MAS for thrips resistance have involved the identification of specific genetic loci and markers linked to tolerance to thrips feeding. Resistance to thrips feeding has been linked to chemical compounds that deter feeding and specific genetic loci for thrips resistance have been identified in chromosome D03 (33).

Challenges in MAS for sucking pest resistance in cotton: Despite the significant potential of MAS, there are several challenges in applying this technology to cotton breeding for pest resistance:

Complexity of resistance traits: Pest resistance is typically controlled by multiple genes with small additive effects, making it challenging to identify and map all relevant QTLs. Emerging solutions like GWAS and genomic selection are helping unravel the complex genetic architecture of sucking pest resistance in cotton. These tools enable the identification of key resistance loci and accelerate the breeding of tolerant varieties by predicting trait performance based on genomic data, even for traits governed by multiple genes.

Environmental influence: Pest resistance is often influenced by environmental factors such as soil type, climate and pest pressure, which can complicate the consistent expression of resistance in the field.

Cost and accessibility: Though MAS technology has significant advantages it is expensive and may not be readily accessible in all breeding programs, especially in developing countries.

MAS has significantly advanced the development of sucking pest-resistant cotton, laying the foundation for next-generation technologies like genetic engineering to further enhance resistance precision and durability.

Genetic engineering for inducing pest resistance in cotton

Genetic engineering offers a promising alternative for developing cotton varieties with enhanced resistance to sucking pests. By introducing specific genes that either deter pests directly or trigger defense responses, genetic engineering provides a more targeted, sustainable approach compared to traditional chemical control. This section focuses on the progress, strategies and key studies in genetic engineering aimed at improving sucking pest resistance in cotton, with numerous references to substantiate the research.

Introduction of insecticidal proteins (cry proteins): The most well-known genetic engineering approach for pest control is the introduction of insecticidal proteins, particularly cry proteins derived from the bacterium *Bacillus thuringiensis* (Bt). These proteins target the gut cells of insect pests, causing them to stop feeding, leading to the pest's death. Although Bt cotton has been primarily developed for controlling lepidopteran pests like bollworms, its effect on sucking pests has also been studied.

Cry proteins against aphids: Cotton plants expressing synthetic insecticidal proteins that target aphids, have been shown to reduce pest feeding, particularly in lab trials (34,35) developed transgenic cotton expressing *Cry1A(c)* and GNA genes, which conferred resistance to *Helicoverpa armigera* and significantly retarded *Aphis gossypii* populations. The integration and expression of these genes were confirmed through molecular biology techniques and insect bioassays.

Expression of plant-derived proteins: In addition to cry proteins, researchers have explored the introduction of other plant-derived proteins that act as pest deterrents. Lectins and defensins are two classes of proteins that have been studied for their effects on sucking pests.

Lectins for aphid resistance: Lectins, which are carbohydrate-binding proteins, have been shown to affect the feeding behavior of aphids. Cotton plants expressing the *Galanthus nivalis* Agglutinin (GNA) lectin have been shown to reduce aphid infestation. GNA disrupts aphid feeding and reproduction by binding to their gut cells (36).

Defensins for whitefly resistance: Defensins, which are small proteins with antimicrobial properties, have been introduced into cotton plants to enhance resistance to whiteflies. Transgenic *Arabidopsis* and cotton plants expressing a modified snowdrop lectin gene (ASGNA) showed resistance to aphids (37).

Transgenic cotton for aphid resistance: Aphids are one of the most damaging pests in cotton cultivation. Genetic engineering strategies have focused on expressing genes that either produce toxic substances that work against aphids or enhance the plant's natural defense mechanisms which are known to inhibit aphid feeding. A previous study showed that transgenic cotton plants expressing *V-ATPase* (vacuolar ATPase) gene experienced a significant reduction in aphid population (38). These studies suggest that genetic engineering can successfully confer aphid resistance in cotton.

Transgenic cotton for whitefly resistance: Whiteflies act as vector for plant viruses and cause direct damage to cotton. Several genetic engineering strategies have been developed to combat whitefly infestations. Research has shown that Bt cotton can reduce populations of whiteflies (particularly *Bemisia tabaci*), a major sucking pest. Whitefly resistance in cotton has been linked to various mechanisms such as antixenosis, antibiosis and tolerance. Cotton genotypes like LRA-5166 and LHDP-1 exhibited strong resistance traits through reduced oviposition and survival rates of whiteflies (39). These phenotypic traits may be supported at the molecular level by PPO-mediated defense pathways, although further research is needed to explicitly connect PPO gene expression to whitefly-specific resistance responses.

Transgenic cotton for mealybug resistance: Mealybugs are another major sucking pest that affects cotton. Use of genetic engineering technique to develop mealy bug-resistant cotton have explored. Several approaches, including the expression of insecticidal proteins or defensive enzymes have proven useful in increasing resistance in plants. Serine protease inhibitors target and inhibit the digestive enzymes in mealybugs, leading to nutrient meal absorption and starvation (40).

Transgenic cotton for thrips resistance: Thrips are an important pest in cotton, particularly in the early stages of growth. The genetically engineered cotton for thrips resistance has mainly

focused on the expression of insecticidal proteins or proteins that disrupt thrips feeding. The cotton chitinase gene, *GhChia*, encodes a protein that may enhance plant resistance to pests like thrips. Its application in cultivating new plant strains can improve crop yield and potentially provide resistance against various agricultural pests (35). Chitinase breaks down chitin in the insect exoskeleton, rendering thrips more susceptible to environmental stress and natural predators. The transgenic cotton showed increased resistance to thrips via feeding damage. The introduction of transgenic traits, such as the Bt *Cry51Aa2.834_16* toxin, has demonstrated effective control of thrips, reducing the need for chemical insecticides and improving yield (41). Additionally, the MON 88702 transgenic event has shown significant efficacy against thrips, providing a viable alternative to traditional pest management strategies (42).

Multi-pest resistance in cotton: To reduce the need for multiple genetic modifications, researchers have focused on creating multi-pest-resistant cotton by integrating genes that provide resistance to a range of sucking pests. Cotton varieties exhibited variable resistance against multiple sucking pests, with significant infestation noted on non-Bt compared to Bt varieties. The population dynamics of pests like jassid, dusky bug and thrips varied across seasons and year (43). Molecular markers were developed for resistance to multiple sucking pests in cotton, specifically targeting aphids, whiteflies, jassids and thrips, using next-generation sequencing and SSR markers to enhance breeding efforts for pest-resistant cotton cultivars (44).

Challenges and future directions in genetic engineering for sucking pest resistance: Despite the promising results, several challenges remain in the genetic engineering of cotton for sucking pest resistance. These mainly include:

Gene flow and resistance management: Concerns about gene flow between genetically modified and non-GM cotton varieties need to be addressed.

Non-target effects: The potential impact of genetically modified cotton on non-target organisms, such as beneficial insects, needs thorough evaluation.

Regulatory approvals: The approval processes for genetically modified crops vary by region, which can hinder the global adoption of genetically engineered pest-resistant cotton.

Farmer adoption: Many farmers, especially smallholders, may hesitate to adopt Genetically Engineered (GE) cotton due to lack of awareness, training or trust in the technology.

Seed cost: GE seeds often come at a premium price, which can be a barrier for resource-limited farmers, affecting the widespread adoption of these technologies.

Intellectual Property (IP) concerns: Patents on GE traits are usually held by private companies, raising concerns over access, affordability and seed-saving restrictions for farmers.

Stacking with RNAi or genome editing: To overcome limitations of single-gene resistance (which pests can often evolve around), researchers are looking to "stack" or combine multiple resistance mechanisms:

RNAi: This technique can silence specific genes in pests (e.g., those needed for feeding or reproduction). Stacking RNAi traits with existing resistance genes could enhance protection and reduce pest survival more effectively.

Genome editing (e.g., CRISPR/Cas9): Unlike traditional transgenic methods, genome editing can precisely modify the plant's own genes (e.g., to enhance defense compound production), reducing pest impact without introducing foreign DNA. This can also reduce regulatory hurdles in some regions.

RNAi for sucking pest control in cotton

RNAi is a revolutionary technique that has shown promising results in managing a wide variety of insect pests, including sucking pests such as aphids, whiteflies, thrips and mealybugs in cotton. RNAi utilizes small RNA molecules, particularly double-stranded RNA (dsRNA), to silence specific genes within a target pest. This leads to a reduction in the pest population, impairing their ability to reproduce, develop or survive. The mechanism by which RNAi operates involves the introduction of dsRNA corresponding to the target gene, which is processed by the RNAi machinery into small interfering RNAs (siRNAs) that guide the degradation of the pest's mRNA, effectively silencing the gene. RNAi represents a sustainable and environmentally friendly alternative to chemical pesticides and offers high specificity by targeting only the pest species, leaving non-target organisms unaffected.

RNAi for aphid resistance in cotton: Several studies have explored RNAi as a method to control aphid populations in cotton. RNAi has been used to silence genes critical to aphid survival, such as genes involved in digestion, reproduction and immunity. By targeting these genes, RNAi reduces aphid feeding efficiency and reproduction, leading to decreased pest populations. Diet-mediated delivery of dsRNA targeting the vacuolar ATPase subunit H (V-ATPase-H) gene in *Aphis gossypii* resulted in significant gene silencing, achieving up to 66.1 % silencing and corresponding mortality rates of 10-63 % (38). RNAi had been used for targeting the chitin synthase 1 (CHS1) gene in *Aphis gossypii*, demonstrating that oral delivery of dsRNA-CHS1 significantly reduces CHS1 expression, leading to increased mortality, decreased longevity and reduced fecundity in aphids (45).

RNAi for whitefly resistance in cotton: RNAi can be utilized to target whitefly genes involved in feeding behavior, immunity and development, providing a non-chemical means of control. RNAi targeting whitefly genes such as *acetylcholinesterase* and *desaturase* genes has been shown to reduce feeding activity, reproduction and overall fitness in whiteflies. RNAi-mediated mortality of the whitefly through transgenic expression of double-stranded RNA homologous to acetyl cholinesterase and ecdysone receptor in tobacco plants suggesting RNAi as a viable option for whitefly control in cotton (46). Silencing the *BtSC5DL* desaturase gene in *Bemisia tabaci* through dsRNA feeding significantly reduced egg production and cholesterol content, demonstrating its crucial role in cholesterol biosynthesis and reproductive capacity, thus offering a potential strategy for whitefly population control (35).

RNAi for mealybug resistance in cotton: RNAi-based strategies have been developed to target genes critical to mealybug development and reproduction. RNAi targeting mealybug genes such as *ecdysone receptor* and *chitinase* genes has been shown to disrupt key biological processes like molting and cuticle formation, leading to increased mortality and decreased reproductive success. RNAi had been used to knock down eight chitinase genes in cotton mealybugs. Knockdown of PsCht4 or PsCht4-1 resulted in molting failure, while silencing PsCht5 caused pupation defects and PsCht10 knockdown led to reduced body size (47).

RNAi for thrips resistance in cotton: Thrips (*Thrips tabaci*) are damaging pests in cotton, causing scarring and deformed flowers due to their feeding behaviour. RNAi-based strategies have been employed to target genes responsible for feeding and development in thrips, effectively reducing their impact on cotton crops. RNAi targeting genes involved in the feeding process, such as *v-ATPase* and *chitinase*, has been shown to reduce thrips survival and feeding efficiency. Silencing the *v-ATPase-B* gene in *Thrips palmi* through RNAi significantly increased mortality (57.03 %) and reduced reproductive fitness (67.73 %), indicating RNAi's potential for effective management of thrips populations in cotton (48).

RNAi for multi-pest resistance in cotton: RNAi has been explored for the simultaneous control of several pest species, including aphids, whiteflies, thrips and mealybugs, by targeting genes that are essential for the survival and reproduction of these pests. RNAi constructs targeting a combination of pest-specific genes can confer resistance to multiple pest species at once, making this strategy more cost-effective and sustainable. A previous study focused on designing fusion double-strand RNAs (dsRNAs) targeting genes from peach aphid and whitefly, rather than specifically on cotton (49). However, the approach can potentially be adapted for managing multiple sap-sucking pests in cotton through RNAi.

Challenges and future directions in RNAi for sucking pest control: Although RNAi has demonstrated great potential in cotton pest management, several challenges remain. Some of these include:

Delivery mechanisms: Efficient and consistent delivery of RNAi constructs to pests is a key challenge. Researchers are working on improving methods for delivering RNAi molecules directly to pests or ensuring that the plant's transgenic RNAi construct is expressed consistently.

Off-target effects: Ensuring that RNAi only targets pest genes without affecting non-target organisms remains a critical concern.

Field efficacy: While laboratory studies show great promise, scaling RNAi-based pest control to field conditions poses challenges related to environmental stability and pest resistance development.

RNAi-based strategies are emerging as powerful tools in IPM for sucking pests in cotton. Stacking RNAi with Bt toxins allows for simultaneous control of both chewing and sucking pests, broadening the pest control spectrum and helping delay resistance development. While Bt is largely ineffective against sucking pests, RNAi targets essential genes in these insects, offering a complementary mode of action. Additionally, combining RNAi with chemical synergists such as low-dose insecticides or nanoparticles that enhance gene silencing can improve RNAi efficiency and reduce chemical input. These RNAi-based combinations strengthen IPM by providing sustainable, targeted and multi-layered pest control solutions.

GWAS for sucking pest resistance in cotton

GWAS have emerged as a powerful tool for identifying genetic loci associated with complex traits, including resistance to sucking pests in cotton. These studies analyze genetic variation across diverse cotton genotypes and link specific genetic markers with the ability to resist various pests, such as aphids, whiteflies, thrips and mealy bugs. This approach provides valuable insights into the

underlying genetic architecture of pest resistance and facilitates the development of genetically improved cotton varieties. By leveraging large-scale genomic data and advanced statistical tools, GWAS can identify both common and rare variants that contribute to pest resistance, offering new avenues for breeding strategies aimed at enhancing cotton's natural defense mechanisms.

Principles and methodology of GWAS in cotton for pest resistance: GWAS is based on the premise that genetic variation in a population is associated with phenotypic traits, including resistance to pests. The approach typically involves the following steps:

Phenotyping: Resistance to sucking pests is measured in a diverse panel of cotton varieties, typically using metrics like pest infestation levels, feeding damage or the presence of pest-resistant traits (e.g., insecticidal proteins).

Genotyping: High-density genotyping platforms (e.g., SNP arrays, whole-genome sequencing) are used to genotype the cotton varieties at thousands to millions of loci across the genome.

Statistical analysis: The relationship between genetic variation (markers) and phenotypic traits is analyzed using statistical tools like mixed linear models, which control for population structure and relatedness.

The GWAS process leads to the identification of specific genomic regions or candidate genes that contribute to pest resistance, providing targets for breeding programs or further molecular studies.

Major findings from GWAS on sucking pest resistance in cotton: Recent GWAS studies on cotton have uncovered several genomic loci and candidate genes associated with resistance to sucking pests. These studies have primarily focused on pests such as aphids, whiteflies and thrips, which are major pests of cotton globally.

GWAS for resistance to aphids: A GWAS on a cotton panel identified 21 significant SNPs associated with genes conferring reduced aphid damage and population growth. Silencing of *GhRem*, *GhLAF1* or *GhCFIm25* notably enhanced aphid reproduction on cotton seedlings. Specifically, the silencing of *GhRem* resulted in a significant reduction in callose deposition, which is likely the underlying cause of the increased susceptibility to *Aphis gossypii*. A previous study identified 12 QTLs related to aphid population and plant response against aphids, with three QTLs qualifying for further analysis (28). Notably, two QTLs on chromosome six (qAG 1,2) overlapped with stem pubescence QTLs, suggesting a link between trichome development and aphid resistance. The genes *TPRI*, *AGO5*, *ZAT5* and *GLO4* were associated with plant defense responses, indicating that SNPs in these regions may contribute to reduced aphid damage and population growth in cotton.

GWAS for whitefly resistance: Genome-wide association mapping identified 39 candidate SNPs associated with cabbage whitefly performance in *Arabidopsis thaliana*, revealing substantial variation in adult survival and oviposition rate and uncovering novel genes not previously linked to plant-insect interactions (50). Nine significant Single Nucleotide Polymorphisms (SNPs) markers were identified to be associated with the nymph count trait on nine chromosomes viz., 2, 4, 8, 10, 11, 12, 13, 15 and 17. Gene annotation analysis revealed the five genes categorized based on their protein structure namely; pentatricopeptide, protein kinase, zinc finger, 2-oxoglutarate (2OG) and Fe (II)-dependent oxygenase, zinc knuckle family proteins and auxin-responsive transcription factor genes, were collectively involved in regulation

of a wide variety of functions ranging from developmental and plant defense-related responses to environmental as well as pathogen attack. The identified significant SNP variants and genes that may be utilized for genomic selection to improve whitefly resistance (51).

GWAS for resistance to thrips: Thirteen clusters of QTL resistant to thrips were detected on 11 chromosomes. Among the 13 QTL clusters, D03 contained a QTL for thrips resistance. It was the first study that mapped the QTL for thrips as well as abiotic resistance (33).

Candidate genes identified in GWAS for sucking pest resistance: Several candidate genes have been identified through GWAS as being associated with resistance to sucking pests in cotton. These genes are often involved in plant defense mechanisms, including the production of secondary metabolites, insecticidal proteins and defense hormones.

Genes related to insecticidal proteins: The *Cry1Ac* and *Cry2A* genes are among the most widely used Bt genes in cotton. These genes produce toxins that are effective against lepidopteran pests. However, their efficacy against sucking pests is limited. Recent studies have shown that double-gene Bt cotton (expressing both *Cry1Ac* and *Cry2A*) can provide better resistance to sucking pests compared to single-gene Bt cotton. For instance, double-gene Bt cotton genotypes have shown higher mortality rates against armyworms and American bollworms compared to single-gene genotype (52). The *Vip3Aa* gene, a second-generation Bt gene, had shown promise in controlling both chewing and sucking pests. When expressed in combination with plant lectins such as ASAL, it has been found to confer resistance to whiteflies and other sucking pests. The *Vip3Aa* gene is particularly useful because it does not share midgut receptor sites with other cry proteins, reducing the likelihood of cross-resistance in pests (14). The *Galanthus nivalis Agglutinin* (GNA) gene, which encodes a plant lectin, has been used in combination with Bt genes to enhance resistance to sucking pests. GNA has been shown to disrupt the feeding behaviour of aphids and other sap-sucking insects. For example, transgenic cotton plants expressing both GNA and *Cry1Ac* have demonstrated significant resistance to aphids and other sucking pests (34,53).

Genes involved in plant defence signalling: A modified GNA gene (ASGNA) has shown significant insecticidal activity against aphids, with a 55 % mortality rate in transgenic plants compared to lower rates in non-modified variants (36). Transgenic cotton expressing protease inhibitors from *Manduca sexta* demonstrated reduced fecundity of the whitefly, indicating a potential strategy for pest management (54).

Genes related to secondary metabolite production:

Flavonoid biosynthesis genes: The genes involved in flavonoid biosynthesis, particularly CHS (chalcone synthase) and F3H (flavanone 3-hydroxylase), play a crucial role in enhancing cotton's resistance to sucking pests. These enzymes are integral to the phenylpropanoid pathway, which produces secondary metabolites that contribute to plant defense mechanisms.

CHS catalyzes the formation of naringenin chalcone, a precursor for various flavonoids, which are vital for plant defense against pests (55). Increased expression of CHS is associated with the accumulation of flavonoids that act as phytoalexins, enhancing resistance to biotic stressors like insect pests (56).

F3H is involved in the conversion of flavanones to dihydroflavonols, further diversifying the flavonoid profile and enhancing the plant's defensive capabilities. Varieties of cotton with higher levels of F3H expression have shown increased tolerance to sucking pests, indicating its importance in pest resistance (57).

Genes related to cell wall strengthening: Cellulose synthase genes are integral to cotton fiber development and plant architecture, contributing to the formation of a strong Secondary Cell Wall (SCW) that can resist pest attacks. The *GhCASPL1* gene, which interacts with the cellulose synthase complex, is crucial for SCW thickening by stabilizing the complex on the plasma membrane, thus enhancing the structural integrity of cotton fibres (58). Functional markers developed for cellulose synthase genes have shown polymorphism between cotton species, indicating their potential use in breeding programs aimed at improving pest resistance (59).

Implications of GWAS for cotton pest resistance breeding: GWAS provides valuable information for improving pest resistance in cotton through MAS and genomic selection. By identifying key loci and candidate genes, GWAS enables breeders to select for pest resistance more efficiently.

Challenges and future directions of GWAS in cotton pest resistance: GWAS has provided significant insights into the genetic basis of pest resistance in cotton, but several challenges need to be addressed:

Complexity of pest resistance: Resistance to sucking pests is a complex trait, influenced by multiple genes and environmental factors. GWAS may not always capture the full genetic variation contributing to pest resistance.

Validation of candidate genes: Further functional validation of candidate genes identified through GWAS is needed to confirm their role in pest resistance.

Polygenic nature of resistance: The polygenic nature of pest resistance means that multiple loci are involved, making it challenging to select for resistance using a small number of markers.

Future studies should focus on integrating GWAS with other technologies, such as transcriptomics, proteomics and metabolomics, to better understand the mechanisms underlying pest resistance and improve breeding strategies for cotton.

Genomic selection for pest resistance

Genomic Selection (GS) influences genome-wide data to predict the breeding value of individuals for pest resistance. This approach is particularly useful for traits controlled by multiple loci with small effects, such as resistance to sucking pests. GS has revolutionized cotton breeding programs by enhancing resistance to sucking pests through genome-wide marker analysis. Unlike traditional MAS, which targets a limited number of QTLs, GS employs genome-wide prediction models to estimate the breeding values of individuals, accounting for both major and minor effect loci (60). This holistic approach is particularly beneficial for complex traits like resistance to aphids (*Aphis gossypii*), jassids (*Amrasca biguttula*), whiteflies (*Bemisia tabaci*) and thrips (*Thrips tabaci*), which are influenced by polygenic inheritance and environmental factors. A previous study discussed the development and validation of molecular markers linked to sucking pest resistance in cotton using next-generation sequencing (44). It highlighted the use of 3450 mapped SSR markers across 26 chromosomes to identify traits of interest.

Additionally, the study involves creating Near Isogenic Lines (NILs) derived from wild relatives of cotton, facilitating GS for pest resistance. This approach aims to enhance breeding strategies for developing resistant cotton cultivars against significant sucking pests like aphids and whiteflies. Further advancements in GS involve integrating phenomic and transcriptomic data, which offers deeper insights into the genetic architecture of pest resistance. GS accelerates the selection process, leading to increased genetic gain per selection cycle. It favours developing high-yielding, stress-tolerant varieties, which can reduce reliance on chemical pesticides in crop breeding (61). Similarly, another study demonstrated that integrating GS into breeding programs could accelerate the development of pest-resistant cultivars, significantly reducing crop losses due to sucking pests (62).

Recent studies have also explored the use of GS for resistance to multiple pests simultaneously. Multi trait models for genomic prediction, emphasizing their ability to account for correlations between traits, which can enhance prediction accuracy for traits like pest resistance in plant and animal breeding, using Bayesian Ridge regression and deep learning frameworks are discussed in another study (63). Despite the initial investment in genomic tools, the long-term benefits in terms of reduced pesticide use and increased yield justify the approach. Additionally, the application of GS in cotton breeding aligns with global efforts to develop climate-resilient and sustainable agricultural practice.

GS has proven to be a valuable tool in cotton breeding programs for enhancing resistance to sucking pests. The integration of genome-wide markers, high-throughput phenotyping and advanced bioinformatics tools allows for accelerated breeding cycles and improved genetic gain, ultimately leading to more resilient and productive cotton cultivars (64,65). As genomic resources and technologies continue to evolve, the future of GS in pest resistance breeding holds significant promise for the cotton industry.

CRISPR/Cas9 and gene editing for pest resistance

CRISPR/Cas9 is a new technology that enables precise modification of genes. In cotton, CRISPR has been used to enhance pest resistance by modifying genes involved in plant defense or editing pest genomes to interfere with their ability to feed or reproduce. The integration of CRISPR/Cas9 genome editing technology will enable precise manipulation of genes responsible for pest resistance, potentially creating new avenues for breeding pest-resistant cotton (31). CRISPR/Cas9 can be utilized to enhance cotton's resistance to sucking pests by editing specific genes associated with pest tolerance. This genetic engineering approach allows for precise modifications, potentially improving cotton's resilience against biotic stresses more efficiently than traditional breeding methods (66). CRISPR/Cas9 system has been utilized to create a mutagenesis library targeting insect-resistance genes in cotton, identifying GhMLP423, which enhances resistance to sucking pests by activating systemic acquired resistance through calcium and reactive oxygen species signalling (67).

CRISPR/Cas9 technology can be used in the following ways to get better pest resistance:

Enhancing plant defense mechanisms: CRISPR/Cas9 can be employed to boost cotton's natural defense mechanisms, such as increasing the production of toxic compounds like gossypol or enhancing the expression of plant proteins that deter pests.

Gossypol production

By editing genes in the cotton genome responsible for gossypol biosynthesis, researchers could develop cotton plants with higher levels of gossypol, which serves as a natural deterrent to many pests, including aphids and whiteflies.

Terpenoid production

Cotton plants can be genetically edited to enhance the production of terpenoids, which are known to deter pests. CRISPR/Cas9 could be used to target these pathways to boost pest resistance.

Production of phenolic compounds

Researchers are exploring the use of CRISPR to increase phenolic compounds in cotton, which play a key role in plant defense by disrupting pest feeding and growth.

Gene editing for plant resistance to aphids: CRISPR/Cas9 could be used to target cotton genes that influence aphid feeding behaviour, leading to reduced aphid attraction and feeding rates.

Use of CRISPR to disrupt pests' feeding mechanisms: In addition to enhancing cotton defences, CRISPR has also been used to modify pest genomes directly. This approach disrupts genes involved in feeding, making pests like aphids less able to feed on transgenic cotton.

Next-Generation Sequencing (NGS) for gene discovery for sucking pest resistance in cotton

NGS has revolutionized genomics by providing a high-throughput, cost-effective approach for genome-wide analysis. NGS has become a critical tool for discovering genes related to various agronomic traits, including resistance to sucking pests in cotton. This technology facilitates the identification of genes involved in plant defense mechanisms, insect resistance pathways and the genetic basis of pest resistance, ultimately supporting the development of cotton varieties with improved pest resistance.

Key discoveries in sucking pest resistance through NGS: NGS has significantly advanced our understanding of the genetic and molecular basis of sucking pest resistance in cotton. Several studies have employed NGS to identify genes involved in resistance to key pests such as aphids, whiteflies and thrips.

Transcriptome profiling for resistance to aphids: Transcriptome profiling revealed 24793 Differentially Expressed Genes (DEGs) in cotton leaves responding to aphid damage, highlighting various resistance mechanisms. This study enhances understanding of cotton's defense responses and aids in developing aphid-resistant cotton cultivars (67). A previous study found GhMYC1374 through aphid-induced cotton transcriptome analysis, revealing its role in enhancing cotton resistance to aphids by activating flavonoid synthesis and free gossypol production, thus contributing to the plant's defense mechanisms against cotton aphids (68). Another study identified 6565 genes differentially expressed in cotton in response to *A. gossypii* feeding and 823 genes for *A. gossypii* (69). Simultaneous feeding led to 2379 genes being expressed, highlighting key pathways involved in cotton's defense mechanisms. Another study identified the R2R3 MYB transcription factor GhMYB18, which enhances cotton's resistance to aphids by regulating the synthesis of flavonoids and activating defense-related enzymes, contributing to the plant's defense response against aphid infestation (70).

RNA-Seq for whitefly resistance in cotton: A study focussed on cotton's resistance to whiteflies (*Bemisia tabaci*) rather than aphids, highlights transcriptomic responses and candidate genes for whitefly resistance, indicating limited information on aphid resistance mechanisms in cotton (68). Another study revealed that aphid infestation in cotton (*Gossypium hirsutum*) alters gene expression, suppressing positive regulators of phytohormonal-induced resistance and activating negative regulators, indicating a complex interaction that facilitates aphid infestation while the plant attempts to mount a defense (71). The study focuses on transcriptomic analysis of *Gossypium hirsutum* in response to whitefly-mediated cotton leaf curl disease, identifying 468 DEGs, which may enhance understanding of temporal gene responses for improving pest resistance in cotton (72).

Differential gene expression in response to thrips: Thousand five hundred DEGs were identified in *Thrips tabaci* populations resistant to spinosad compared to susceptible populations. The *de novo* transcriptome analysis revealed 25552 unigenes, with significant genes including cytochrome P450 and vitellogenin. The expression of cytochrome P450 increased with resistance levels, while higher vitellogenin expression correlated with increased fecundity in resistant populations, indicating a potential link between gene expression and resistance mechanisms in *T. tabaci* (73). Differential expression of microRNAs (miRNAs) were studied in *Thrips tabaci*, particularly in pupal and adult stages. Notably, miRNAs such as tta-miR-281, tta-miR-184, tta-miR-3533, tta-miR-N1, tta-miR-N7 and tta-miR-N9 showed higher expression levels, suggesting their involvement in larval and adult development, metamorphosis, parthenogenesis and reproduction (74). This research provides insights into the regulatory roles of miRNAs in gene expression, contributing to our understanding growth and development of *T. tabaci*.

Whole-genome resequencing for pest resistance loci: A locus linked to *Verticillium* wilt resistance was identified, showing differential expression in response to pathogens and insects, thus regulating metabolic pathways crucial for resistance (75). A core collection of upland cotton was resequenced, revealing 3.66 million SNPs associated with fibre quality and yield, which also included loci relevant to pest resistance (76). The study utilized Genotyping by Sequencing (GBS) to identify QTLs for trichome-based pest resistance in cotton, revealing significant loci on chromosome A06 associated with leaf and stem pubescence, enhancing understanding of pest-host interactions and aiding breeding programs (28).

De novo genome assembly for sucking pest resistance: The *Gossypium stocksii* genome assembly provides a valuable resource for understanding resistance to CLCuV caused by *Bemisia tabaci*, a significant pest. This high-quality genome can facilitate breeding programs aimed at enhancing pest resistance in cotton cultivars (77). *De novo* chromosome-level genome assemblies of two *Aphis gossypii* biotypes, reveal genomic variations that contribute to host adaptation and potential insecticide resistance, which are crucial for developing strategies against sucking pest resistance in cotton (78). A high-quality chromosome-level genome assembly of the cotton thrips, *Thrips tabaci*, had been presented which aids in understanding its biology and developing management strategies, potentially contributing to resistance against sucking pests in cotton crops (79).

Future directions in using NGS for pest resistance in cotton: NGS technologies continue to evolve and improve, providing even greater opportunities for gene discovery in cotton. Future research will likely focus on the following:

Integrated omics approaches: Combining NGS with transcriptomics, proteomics and metabolomics can provide a holistic understanding of how cotton responds to sucking pest attacks, allowing for the identification of key genes and metabolites involved in pest resistance.

CRISPR and gene editing: NGS data can be integrated with CRISPR technology to edit specific genes associated with pest resistance. This can be done by identifying candidate genes through NGS and then using CRISPR-Cas9 to introduce beneficial mutations in cotton cultivars.

Improved genome assemblies: As NGS technology advances, more complete and accurate genome assemblies will be produced for cotton varieties, improving the identification of pest-resistant loci.

Transcriptomics for functional insights: Transcriptomics, which involves studying the RNA transcripts expressed in a cell or tissue, provides valuable insights into pest-responsive gene networks (67,70,80).

RNA Sequencing (RNA-Seq): RNA-Seq has identified DEGs in resistant and susceptible cotton varieties under pest attack (68,71,73,74).

Non-coding RNAs: miRNAs and long non-coding RNAs (lncRNAs) regulate key resistance pathways. lncRNAs play crucial roles in cotton's defense against sap-sucking insects. A previous study identified lncA07 and lncD09 as key regulatory lncRNAs, influencing jasmonic acid levels and susceptibility to insect infestation in cotton cultivars (81). Another study identified the lncRNAs; GhlncRNA149.1 as a positive regulator in cotton's defense against cotton aphids, enhancing resistance through the up-regulation of antioxidant enzymes and defense-related genes, thereby improving the plant's response to aphid damage (69).

Temporal transcriptomics: Studies on stage-specific gene expression have revealed critical windows for pest resistance responses. Temporal transcriptomics in cotton revealed that aphids and whiteflies alter gene expression rapidly, with significant changes observed within 2 hr of infestation. This includes suppression of resistance genes and induction of pathways related to amino acid and carbohydrate metabolism (71). Temporal transcriptomics in cotton revealed differential gene expression at 0, 12, 24 and 48 hr post-whitefly infestation, identifying key defense-related genes, including protein kinases and transcription factors, crucial for enhancing resistance against sucking pests like *Bemisia tabaci* (68).

Proteomics and metabolomics: Proteomics and metabolomics complement genomics transcriptomics by identifying proteins and metabolites involved in pest defense. The study focussed on label-free quantitative proteomics to identify differentially expressed proteins in cotton genotypes resistant to leafhopper. It highlighted pathways like carbon fixation and metabolism, crucial for understanding molecular mechanisms underlying pest resistance (82).

Systems biology approaches: Systems biology approaches provide holistic frameworks for understanding and managing sap-sucking pests by integrating multi-scale data (genomic, proteomic, metabolic) to decipher plant-insect interactions and develop

targeted control strategies. Computational models are being developed to predict the interaction of genes, proteins and metabolites in pest defense. Systems biology approaches shift pest management from reactive to predictive by unifying molecular mechanisms with ecological interactions, enabling sustainable solutions like precision RNAi and optimized biocontrol.

Development of molecular markers: Molecular markers linked to pest resistance traits enable rapid and cost-effective screening of cotton germplasm. Molecular markers linked to sucking pest resistance have been developed in cotton using NGS, rather than de novo genome assembly (44). It utilizes mapped SSR markers and aims to identify SNP-based markers for enhanced pest resistance traits. The study identified two SSR molecular markers linked to jassid resistance in cotton: BNL1646 and DOW047, which exhibited significant LOD values of 4.5 and 7.2 and PVE % of 6.6 and 10.3, respectively, aiding in MAS (83). CIR139 is the polymorphic SSR marker identified in the study, which differentiates hybrids from parental lines CO17 and KC3. This marker is crucial for establishing a mapping population for QTL mapping of anatomical features conferring sucking pest resistance. The study identified the JESPR 154 primer, which amplified a 150 bp fragment linked to the hairiness trait in resistant cotton genotypes (KC 3, GTHV 15-34, GISV 323, RHC 1409), indicating potential resistance genes against jassids (84).

Identification of resistance genes: Advances in functional genomics have facilitated the discovery of resistance (R) genes and transcription factors regulating pest tolerance. i R2R3 MYB transcription factor GhMYB18 was identified in cotton, which enhances resistance to aphids by activating defense-related enzymes and inducing the synthesis of salicylic acid and flavonoids, thereby modulating the plant's defense response against aphid attack (70). Several candidate insect-resistant genes have been in cotton through transcriptome analysis comparing a Highly Resistant cultivar (HR) and a highly susceptible cultivar (ZS) to whitefly infestation (68). Key findings highlighted hub genes such as WRKY40 and copper transport protein, which may regulate cotton defenses. Silencing *GhMPK3* demonstrated its role in the MPK-WRKY-JA and ET pathways, leading to increased susceptibility, thus confirming the potential of these genes for enhancing whitefly resistance in cotton. partially dominant hairiness gene H1, which is linked to minor hairiness genes and the hair density gene H2, responsible for the dense tomentum were found in *G. tomentosum* (18).

Challenges in genomic approaches: Despite these advances, several challenges need to be addressed for the success of this approach.

- The polyploid nature of cotton complicates genome assembly and gene annotation.
- Pest resistance is often controlled by complex polygenic traits, making QTL mapping and MAS challenging.
- High costs of multi-omics studies limit their adoption in resource-constrained breeding programs.

Challenges in achieving sucking pest resistance

Breeding cotton for pest resistance holds significant promise for reducing reliance on chemical pesticides and improving sustainable crop production. However, the process is fraught with multiple challenges that must be carefully addressed for effective and long-term success. Some of the key challenges include:

Complexity of resistance traits:

- Pest resistance in cotton is rarely governed by a single gene. Instead, it is often a polygenic trait, involving the interaction of multiple genes across various pathways.
- The quantitative nature of resistance makes it difficult to identify, transfer and stabilize resistance traits using conventional breeding techniques.
- MAS and genomic tools are helping to address this, but these approaches require significant investment and technical expertise.

Pest evolution and adaptation:

- Pests like aphids and whiteflies, exhibit high reproductive rates and genetic plasticity, allowing them to rapidly adapt to resistance mechanisms in host plants.
- The breakdown of resistance over time due to pest evolution is a major concern, as has been observed in cases of Bt cotton where target pests developed resistance.
- Continuous monitoring and integrating resistance management strategies (e.g., gene pyramiding, crop rotation, refuge crops) are essential to prolong the effectiveness of resistance traits.

Environmental variability:

- The expression and effectiveness of pest resistance traits can be influenced by environmental conditions such as temperature, humidity, soil fertility and rainfall.
- A variety that is resistant under one set of conditions may not perform equally well in another, limiting its geographical adaptability.
- Pest pressure also varies across regions and seasons, necessitating location-specific breeding efforts and multi-location trials.

Farmer adoption barriers:

Even when resistant varieties are successfully developed, adoption by farmers is not guaranteed.

- Cost: Resistant varieties may be more expensive due to the use of advanced breeding technologies or proprietary traits.
- Knowledge gap: Farmers may lack awareness or understanding of the benefits of pest-resistant varieties or the best agronomic practices for their use.
- Cultural preferences: Some farmers prefer traditional or locally adapted varieties for their yield stability, taste or fibre quality, even if they are more susceptible to pests.
- Extension services, demonstrations and economic incentives are critical to overcoming these barriers and encouraging widespread adoption.

Future directions

To enhance pest-tolerance in cotton breeding, some other methodologies such as pangenomics, can be checked keeping in mind the further scope of improvement.

Constructing a pangenome for cotton is a powerful approach to capture the full spectrum of genetic diversity related to pest resistance, enabling the identification of novel alleles and resistance genes across diverse genotypes. This genomic foundation supports precision breeding, where the integration of CRISPR/Cas genome editing with MAS accelerates the development of pest-tolerant varieties by allowing precise modification and efficient selection of key resistance traits. However, to ensure these advances translate into practical benefits, field validation is essential testing genetically improved lines under diverse agro-climatic conditions confirms the stability, effectiveness and adaptability of pest resistance traits in real-world farming systems.

Conclusion

Sucking pest tolerance in cotton is a complex but crucial aspect of improving cotton production sustainability. By focusing on developing crops that can withstand pest attacks without significant yield loss, breeders can help reduce reliance on chemical pesticides and contribute to more environmentally friendly farming practices. In India, varieties like KC 2, DHY 286, Khandwa 2, B 1007 and PKV 081 were developed through artificial screening and JR 23 developed through conventional pedigree breeding method, specifically a three-way cross involving the varieties LRA 5166 (CCH 526612 X HLS 329) for jassid resistance in cotton. Whitefly resistant varieties like, LK 861 and Kanchana and aphid resistant varieties including Bahtim 1 and JMD were developed through selection followed by hybridization. Field screening of *Gossypium sylvestre* genotypes identified DGS-18, DGS-26 and DGS-28 as highly resistant to mealybugs. These lines offer valuable genetic resources for breeding cotton varieties with enhanced mealybug tolerance. While significant progress has been made in identifying resistance mechanisms and developing new breeding strategies, challenges remain in dealing with pest adaptation and the multi-faceted nature of pest resistance. Despite the challenges associated with this strategy, advancements in genetic technologies and a deeper understanding of plant-pest interactions are driving progress in this field. The integration of conventional breeding with advanced biotechnological techniques, such as MAS and CRISPR/Cas9, holds great potential for creating resilient cotton varieties because it combines the broad, time-tested genetic base of traditional breeding with the precision and speed of modern tools. However, continuous research, innovative breeding strategies and the incorporation of diverse pest management practices will be essential to ensure long-term success in combating sucking pests in cotton production.

Authors' contributions

MS collected the literature and wrote the draft. RS, PN, MBN, SN and UD have reviewed this article for publication. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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References

- Simair AA, Simair SP. Status and recent progress in determining the genetic diversity and phylogeny of cotton crops. In: Patil NB, editor. Cotton science and processing technology: Gene, ginning, garment and green recycling. Singapore: Springer; 2020. p. 15-37 https://doi.org/10.1007/978-981-15-9169-3_2
- Rojo-Gutiérrez E, Buenrostro-Figueroa J, López-Martínez L, Sepúlveda D, Baeza-Jiménez R. Biotechnological potential of cottonseed, a by-product of cotton production. In: Bhaskar T, Pandey A, Mohan SV, Lee DJ, Khanal SK, editors. Valorisation of agro-industrial residues. Vol II: Non-biological approaches. Cham: Springer; 2020. p. 63-82 https://doi.org/10.1007/978-3-030-39208-6_3
- Razzaq A, Zafar MM, Ali A, Li P, Qadir F, Zahra LT, et al. Biotechnology and solutions: insect-pest-resistance management for improvement and development of Bt cotton (*Gossypium hirsutum* L.). Plants. 2023;12(23):4071. <https://doi.org/10.3390/plants12234071>
- Shera P, Kumar V, Jindal V. Sucking pests of cotton. In: Arora R, editor. Sucking pests of crops. Singapore: Springer; 2020. p. 249-84 https://doi.org/10.1007/978-981-15-6149-8_8
- Chohan SM, Sohail MS, Sharif I. Sustainable pest management strategies for cotton crop in Pakistan: a review. J Agric Res. 2024;62(3):181-92.
- Rauf S, Shehzad M, Al-Khayri JM, Imran HM, Noorka IR. Cotton (*Gossypium hirsutum* L.) breeding strategies. In: Al-Khayri JM, Jain SM, Johnson DV, editors. Advances in plant breeding strategies: Industrial and food crops. Cham: Springer; 2019. p. 29-59. https://doi.org/10.1007/978-3-030-23265-8_2
- Mitchell C, Brennan RM, Graham J, Karley AJ. Plant defense against herbivorous pests: exploiting resistance and tolerance traits for sustainable crop protection. Front Plant Sci. 2016;7:1132. <https://doi.org/10.3389/fpls.2016.01132>
- da Silva PvdC, Junior CB, Goncalves de Jesus F, Hoffmann LV, Pinto de Menezes IP. Antixenosis in cotton genotypes (*Gossypium hirsutum* var. marie galante) to *Spodoptera frugiperda* (Lepidoptera: Noctuidae) mediated by trichome and gossypol densities. Aust J Crop Sci. 2021;15(12):1435-41. <https://doi.org/10.21475/ajcs.21.15.12.p3310>
- Robinson S, Wolfenbarger D, Dilday R. Antixenosis of smooth leaf cotton to the ovipositional response of tobacco budworm. Crop Sci. 1980;20(5):646-9. <https://doi.org/10.2135/cropsci1980.0011183X0020000500026x>
- Parrott W, Jenkins N, McCarthy J Jr, Lambert L. A procedure to evaluate antibiosis in cotton to the tobacco budworm. J Econ Entomol. 1978;71(2):310-2. <https://doi.org/10.1093/jee/71.2.310>
- Singh V, Mandhania S, Pal A, Kaur T, Banakar P, Sankaranarayanan K, et al. Morpho-physiological and biochemical responses of cotton (*Gossypium hirsutum* L.) genotypes upon sucking insect-pest infestations. Physiol Mol Biol Plants. 2022;28(11):2023-39. <https://doi.org/10.1007/s12298-022-01253-w>
- Aherkar SS, Deshmukh SB, Konde NM, Paslawar AN, Joshi T, Messmer MM, et al. Studies on morphophysiological and biochemical parameters for sucking pest tolerance in organic cotton. Agriculture. 2023;13(7):1402. <https://doi.org/10.3390/agriculture13071402>
- Sarker U. Variability, heritability, character association and path coefficient analysis in advanced breeding lines of rice (*Oryza sativa* L.). Genetika. 2020;52(2):711-26. <https://doi.org/10.2298/GENS2002711H>
- Din SU, Azam S, Rao AQ, Shad M, Ahmed M, Gul A, et al. Development of broad-spectrum and sustainable resistance in cotton against major insects through combination of Bt and plant lectin genes. Plant Cell Rep. 2021;40:707-21. <https://doi.org/10.1007/s00299-021-02669-6>
- Dhamayanthi K, Rameash K, Manivannan A, Sheeba A, Abirami S. Studies on leaf hairiness and sucking pest resistance in Egyptian cotton (*Gossypium barbadense* L.). J Cotton Res Dev. 2020;34(2):204-8.
- Sarwar M, Hamed M, Yousaf M, Hussain M. Identification of resistance to insect pest infestations in cotton (*Gossypium hirsutum* L.) varieties evaluated in field experiments. Int J Sci Res Environ Sci. 2013;1(11):317-23. <https://doi.org/10.12983/ijres-2013-p317-323>
- Rajashekhar M, Katageri I, Khadi B. In vivo interspecific cross recovery among different cotton (*Gossypium* spp.). Indian J Genet Plant Breed. 2005;65(1):23-8.
- Knight RL. The genetics of jassid resistance in cotton: I. The genes H1 and H2. J Genet. 1952;51:47-66. <https://doi.org/10.1007/BF02986704>
- Miyazaki J, Stiller WN, Wilson LJ. Sources of plant resistance to thrips: a potential core component in cotton IPM. Entomol Exp Appl. 2017;162(1):30-40. <https://doi.org/10.1111/eea.12501>
- Ismail SM. Gossypol as a natural insecticide in cotton plants against cotton thrips and pink bollworm. Prog Chem Biochem Res. 2021;4:68-79.
- Rizwan M, Abro S, Asif MU, Hameed A, Mahboob W, Deho ZA, et al. Evaluation of cotton germplasm for morphological and biochemical host plant resistance traits against sucking insect pest complex. J Cotton Res. 2021;4(1):1-8. <https://doi.org/10.1186/s42397-021-00093-5>
- Perveen SS, Qaisrani T, Siddiqui F, Perveen R, Naqvi S. Cotton plant volatiles and insect behavior. Pak J Biol Sci. 2001;4(5):554-8. <https://doi.org/10.3923/pjbs.2001.554.558>
- Farhan M, Pan J, Hussain H, Zhao J, Yang H, Ahmad I, et al. Aphid-resistant plant secondary metabolites: types, insecticidal mechanisms and prospects for utilization. Plants. 2024;13(16):2332. <https://doi.org/10.3390/plants13162332>
- Vonzun S, Messmer MM, Boller T, Shrivats Y, Patil SS, Riar A. Extent of bollworm and sucking pest damage on modern and traditional cotton species and potential for breeding in organic cotton. Sustainability. 2019;11(22):6353. <https://doi.org/10.3390/su11226353>
- Jindal V, Arora R, Kumar R. Screening of cotton genotypes for resistance to sucking pests. Ann Plant Prot Sci. 2007;15(1):26-9.
- Shrestha N, Bertone M, Bowman DT, Kuraparthi V. Breeding, genetics and genomics of cotton. In: Cotton breeding and biotechnology. Cham: Springer; 2021. p. 89-112
- Jindal S, Pathak D, Pandher S, Rathore P, Vikal Y. Inheritance and molecular tagging of genes introgressed from *Gossypium arboreum* to *G. hirsutum* for leafhopper tolerance. J Genet. 2022;101(2):42. <https://doi.org/10.1007/s12041-022-01379-6>
- Ahmed H, Nazir MF, Pan Z, Gong W, Iqbal MS, He S, et al. Genotyping by sequencing revealed QTL hotspots for trichome-based plant defense in *Gossypium hirsutum*. Genes. 2020;11(4):368. <https://doi.org/10.3390/genes11040368>
- An Q, Pan Z, Aini N, Han P, Wu Y, You C, et al. Identification of candidate genes for aphid resistance in upland cotton by QTL mapping and expression analysis. Crop J. 2023;11(5):1600-4. <https://doi.org/10.1016/j.cj.2023.03.006>
- Yang J, Zhang H, Chen H, Sun Z, Ke H, Wang G, et al. Genome-wide association study reveals novel SNPs and genes in *Gossypium hirsutum* underlying *Aphis gossypii* resistance. Theor Appl Genet. 2023;136(8):171. <https://doi.org/10.1007/s00122-023-04415-w>
- Zhang B, Rahman MU. Targeted breeding in cotton using CRISPR/Cas9 genome editing. In: Zhang B, editor. Cotton precision breeding. Cham: Springer; 2021. p. 313-27 https://doi.org/10.1007/978-3-030-64504-5_14
- Sattar MN, Javed M, Hussain SB, Babar M, Chee PW, Iqbal Z, et al. Mapping of quantitative trait loci controlling cotton leaf curl disease resistance in upland cotton. Plant Breed. 2023;142(2):247-57. <https://doi.org/10.1111/pbr.13084>
- Abdelraheem A, Kuraparthi V, Hinze L, Stelly D, Wedegaertner T, Zhang J. Genome-wide association study for tolerance to drought and salt and resistance to thrips at the seedling growth stage in

- US upland cotton. *Ind Crops Prod.* 2021;169:113645. <https://doi.org/10.1016/j.indcrop.2021.113645>
34. Khabbazi SD, Khabbazi AD, Özcan SF, Bakhsh A, Başalma D, Özcan S. Expression of GNA and biting site-restricted CryIac in cotton: an efficient attribution to insect pest management strategies. *Plant Biotechnol Rep.* 2018;12:273-82. <https://doi.org/10.1007/s11816-018-0493-8>
 35. Liu Y, Gong C, Hu Y, Han H, Tian T, Luo Y, et al. Silencing of the plant-derived horizontally transferred gene BtSC5DL effectively controls *Bemisia tabaci* MED. *Pest Manag Sci.* 2023;79(5):1863-72.
 36. He P, Jia H, Xue H, Zeng Y, Tian L, Hu X, et al. Expression of modified snowdrop lectin (*Galanthus nivalis* agglutinin) protein confers aphid and *Plutella xylostella* resistance in *Arabidopsis* and cotton. *Genes.* 2022;13(7):1169. <https://doi.org/10.3390/genes13071169>
 37. Wang ZZ, Shi M, Ye XQ, Chen MY, Chen XX. Identification, characterization and expression of a defensin-like antifungal peptide from the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae). *Insect Mol Biol.* 2013;22(3):297-305. <https://doi.org/10.1111/imb.12021>
 38. Rebijith K, Asokan R, Ranjitha H, Rajendra Prasad B, Krishna V, Krishna Kumar N. Diet-delivered dsRNAs for juvenile hormone-binding protein and vacuolar ATPase-H implied their potential in the management of the melon aphid (Hemiptera: Aphididae). *Environ Entomol.* 2016;45(1):268-75. <https://doi.org/10.1093/ee/nvv178>
 39. Tamilselvan R, Mahalingam C, Mohankumar S, Senguttuvan K. Characterization of resistance mechanisms to the whitefly, *Bemisia tabaci* Asia-II-8 (Hemiptera: Aleyrodidae) in cotton genotypes. *Int J Trop Insect Sci.* 2021;41(1):373-81. <https://doi.org/10.1007/s42690-020-00215-7>
 40. Ryan C. Proteinase inhibitors. In: Conn EE, Stumpf PK, editors. *Proteins and nucleic acids.* New York: Academic Press; 1981. p. 351-70 <https://doi.org/10.1016/B978-0-12-675406-3.50015-3>
 41. Graham SH, Stewart SD. Field study investigating Cry51Aa2.834_16 in cotton for control of thrips (Thysanoptera: Thripidae) and tarnished plant bugs (Hemiptera: Miridae). *J Econ Entomol.* 2018;111(6):2717-26. <https://doi.org/10.1093/jee/toy250>
 42. Akbar W, Gowda A, Ahrens JE, Stelzer JW, Brown RS, Bollman SL, et al. First transgenic trait for control of plant bugs and thrips in cotton. *Pest Manag Sci.* 2019;75(3):867-77. <https://doi.org/10.1002/ps.5234>
 43. Ali A, Akhtar MN, Awan MQ, Ali A, Farooq A. Behavioural response of cotton (*Gossypium hirsutum*) against the infestation of different sucking insect pests in Southern Punjab, Pakistan. *Pure Appl Biol.* 2020;10(1):124-31. <https://doi.org/10.19045/bspab.2021.100014>
 44. Sridhar V, Reddy PS, Reddy SS, Satihal MB, Prasad MS, Kumar VR, et al. Development and validation of molecular markers for sucking pest resistance in cotton. *Can J Biotechnol.* 2017;1 (Special):288. <https://doi.org/10.24870/cjb.2017-a272>
 45. Ullah F, Gul H, Wang X, Ding Q, Said F, Gao X, et al. RNAi-mediated knockdown of chitin synthase 1 (CHS1) gene causes mortality and decreased longevity and fecundity in *Aphis gossypii*. *Insects.* 2019;11(1):22. <https://doi.org/10.3390/insects11010022>
 46. Malik HJ, Raza A, Amin I, Scheffler JA, Scheffler BE, Brown JK, et al. RNAi-mediated mortality of the whitefly through transgenic expression of double-stranded RNA homologous to acetylcholinesterase and ecdysone receptor in tobacco plants. *Sci Rep.* 2016;6(1):38469. <https://doi.org/10.1038/srep38469>
 47. Omar MA, Ao Y, Li M, He K, Xu L, Tong H, et al. Functional difference of eight chitinase genes between male and female of the cotton mealybug, *Phenacoccus solenopsis*. *Insect Mol Biol.* 2019;28(4):550-67. <https://doi.org/10.1111/imb.12572>
 48. Rakesh V, Singh A, Ghosh A. Suppression of *Thrips palmi* population by spray-on application of dsRNA targeting V-ATPase-B. *Int J Biol Macromol.* 2024;280:135576. <https://doi.org/10.1016/j.ijbiomac.2024.135576>
 49. Xu Q-Q, Shang F, Feng S-Y, Xie Q-P, Zhang W, Wang Z-G, et al. Design of fusion double-strand RNAs to control two global sap-sucking pests. *Pestic Biochem Physiol.* 2024;205:106114. <https://doi.org/10.1016/j.pestbp.2024.106114>
 50. Broekgaarden C, Bucher J, Bac-Molenaar J, Keurentjes JJ, Kruijer W, Voorrips RE, et al. Novel genes affecting the interaction between the cabbage whitefly and *Arabidopsis* uncovered by genome-wide association mapping. *PLoS One.* 2015;10 (12):e0145124. <https://doi.org/10.1371/journal.pone.0145124>
 51. Samanya L. Genetic analysis of resistance to African cassava whitefly, *Bemisia tabaci*, in crosses of Latin American by Ugandan cassava parental lines. Master of Science [thesis]. Kampala: Makerere University; 2024
 52. Amjad M, Cheema HMN, Ahmad JN, Noor K, Alvi HA, Ahmad H, et al. Evaluation of resistance and susceptibility level of single and double gene Bt cotton against armyworm and American bollworm. *Int J Appl Exp Biol.* 2024;3(1):83-91. <https://doi.org/10.56612/ijaaeb.v3i1.69>
 53. Liu Z, Zhu Z, Zhang T. Development of transgenic CryIA(c)+GNA cotton plants via pollen tube pathway method confers resistance to *Helicoverpa armigera* and *Aphis gossypii* Glover. In: Zhang BH, editor. *Transgenic cotton: methods and protocols.* New York: Springer; 2012. p.199-210 https://doi.org/10.1007/978-1-62703-212-4_17
 54. Thomas JC, Adams DG, Keppenne VD, Wasmann CC, Brown JK, Kanost MR, et al. Protease inhibitors of *Manduca sexta* expressed in transgenic cotton. *Plant Cell Rep.* 1995;14:758-62. <https://doi.org/10.1007/BF00232917>
 55. Martin C. Structure, function and regulation of the chalcone synthase. *Int Rev Cytol.* 1993;147:233-84. [https://doi.org/10.1016/S0074-7696\(08\)60770-6](https://doi.org/10.1016/S0074-7696(08)60770-6)
 56. Dao T, Linthorst H, Verpoorte R. Chalcone synthase and its functions in plant resistance. *Phytochem Rev.* 2011;10:397-412. <https://doi.org/10.1007/s11101-011-9211-7>
 57. Dixit G, Srivastava A, Rai KM, Dubey RS, Srivastava R, Verma PC. Distinct defensive activity of phenolics and phenylpropanoid pathway genes in different cotton varieties toward chewing pests. *Plant Signal Behav.* 2020;15(5):1747689. <https://doi.org/10.1080/15592324.2020.1747689>
 58. Zhang L, Wen X, Chen X, Zhou Y, Wang K, Zhu Y. GhCASPL1 regulates secondary cell wall thickening in cotton fibers by stabilizing the cellulose synthase complex on the plasma membrane. *J Integr Plant Biol.* 2024;66(12):2632-47. <https://doi.org/10.1111/jipb.13777>
 59. Lin Z, Wang Y, Zhang X, Zhang J. Functional markers for cellulose synthase and their comparison to SSRs in cotton. *Plant Mol Biol Rep.* 2012;30:1270-5. <https://doi.org/10.1007/s11105-012-0432-8>
 60. Meuwissen TH, Hayes BJ, Goddard M. Prediction of total genetic value using genome-wide dense marker maps. *Genetics.* 2001;157 (4):1819-29. <https://doi.org/10.1093/genetics/157.4.1819>
 61. Bhuvaneswari R, Saravanan K, Vennila S, Suganthi S. Advances in genomic selection for enhanced crop improvement: bridging the gap between genomics and plant breeding. *Plant Sci Arch.* 2020;1 (1):1-10. <https://doi.org/10.51470/PSA.2020.5.1.11>
 62. Crossa J, Pérez-Rodríguez P, Cuevas J, Montesinos-López O, Jarquín D, De Los Campos G, et al. Genomic selection in plant breeding: methods, models and perspectives. *Trends Plant Sci.* 2017;22(11):961-75. <https://doi.org/10.1016/j.tplants.2017.08.011>
 63. Montesinos-López OA, Montesinos-López A, Mosqueda-Gonzalez BA, Montesinos-López JC, Crossa J. Accounting for correlation between traits in genomic prediction. In: Varshney RK, Roorkiwal M, Sorrells ME, editors. *Genomic prediction of complex traits: Methods and protocols.* New York: Springer; 2022. p.285-327 https://doi.org/10.1007/978-1-0716-2205-6_10

64. Heffner EL, Lorenz AJ, Jannink JL, Sorrells ME. Plant breeding with genomic selection: gain per unit time and cost. *Crop Sci.* 2010;50(5):1681-90. <https://doi.org/10.2135/cropsci2009.11.0662>
65. Poland J, Rutkoski J. Advances and challenges in genomic selection for disease resistance. *Annu Rev Phytopathol.* 2016;54:79-98. <https://doi.org/10.1146/annurev-phyto-080615-100056>
66. Ahmed AI, Khan AI, Negm MA, Iqbal R, Azhar MT, Khan SH, et al. Enhancing cotton resilience to challenging climates through genetic modifications. *J Cotton Res.* 2024;7(1):10. <https://doi.org/10.1186/s42397-024-00171-4>
67. Zhong X, Yang Y, Feng P, Ma Q, Su Q, Wang X, et al. Transcriptomic profiling of cotton leaves in response to cotton aphid damage. *Acta Physiol Plant.* 2022;44(10):98. <https://doi.org/10.1007/s11738-022-03438-y>
68. Li J, Zhu L, Hull JJ, Liang S, Daniell H, Jin S, et al. Transcriptome analysis reveals a comprehensive insect resistance response mechanism in cotton to infestation by the phloem-feeding insect *Bemisia tabaci* (whitefly). *Plant Biotechnol J.* 2016;14(10):1956-75. <https://doi.org/10.1111/pbi.12554>
69. Zhang Y, Hu Z, Zhang H, Zeng M, Chen Q, Wang H, et al. The long non-coding RNA GhLncRNA149.1 improves cotton defense response to aphid damage as a positive regulator. *Plant Cell Tissue Organ Cult.* 2023;152(3):517-27. <https://doi.org/10.1007/s11240-022-02424-z>
70. Hu Z, Zhang J, Zhong X, Feng W, Zhang H, Luo X, et al. An R2R3 MYB transcription factor GhMYB18 confers cotton aphid resistance through regulating the synthesis of flavonoids in cotton plants. *bioRxiv*; 2022. <https://doi.org/10.21203/rs.3.rs-1371290/v1>
71. Dubey NK, Goel R, Ranjan A, Idris A, Singh SK, Bag SK, et al. Comparative transcriptome analysis of *Gossypium hirsutum* L. in response to sap-sucking insects: aphid and whitefly. *BMC Genomics.* 2013;14:241. <https://doi.org/10.1186/1471-2164-14-241>
72. Naqvi RZ, Zaidi SS, Mukhtar MS, Amin I, Mishra B, Strickler S, et al. Transcriptomic analysis of cultivated cotton *Gossypium hirsutum* provides insights into host responses upon whitefly-mediated transmission of cotton leaf curl disease. *PLoS One.* 2019;14(2):e0210011. <https://doi.org/10.1371/journal.pone.0210011>
73. Rosen R, Lebedev G, Kontsedalov S, Ben-Yakir D, Ghanim M. A de novo transcriptomics approach reveals genes involved in *Thrips tabaci* resistance to spinosad. *Insects.* 2021;12(1):67. <https://doi.org/10.3390/insects12010067>
74. Balan RK, Ramasamy A, Hande RH, Gawande SJ, Krishna Kumar NK. Genome-wide identification, expression profiling and target gene analysis of microRNAs in the onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), vectors of tospoviruses (Bunyaviridae). *Ecol Evol.* 2018;8(13):6399-419. <https://doi.org/10.1002/ece3.3762>
75. Chen B, Zhang Y, Sun Z, Liu Z, Zhang D, Yang J, et al. Tissue-specific expression of GhnsLTPs identified via GWAS sophisticatedly coordinates disease and insect resistance by regulating metabolic flux redirection in cotton. *Plant J.* 2021;107(3):831-46. <https://doi.org/10.1111/tpj.15349>
76. Ma Z, He S, Wang X, Sun J, Zhang Y, Zhang G, et al. Resequencing a core collection of upland cotton identifies genomic variation and loci influencing fiber quality and yield. *Nat Genet.* 2018;50(6):803-13. <https://doi.org/10.1038/s41588-018-0119-7>
77. Grover CE, Yuan D, Arick MA, Miller ER, Hu G, Peterson DG, et al. The *Gossypium stocksii* genome as a novel resource for cotton improvement. *G3 (Bethesda).* 2021;11(7):jkab125. <https://doi.org/10.1093/g3journal/jkab125>
78. Zhang S, Gao X, Wang L, Jiang W, Su H, Jing T, et al. Chromosome-level genome assemblies of two cotton-melon aphid *Aphis gossypii* biotypes unveil mechanisms of host adaptation. *Mol Ecol Resour.* 2022;22(3):1120-34. <https://doi.org/10.1111/1755-0998.13521>
79. Gao Y, Ji J, Xu C, Wang L, Zhang K, Li D, et al. Chromosome-level genome assembly of cotton thrips *Thrips tabaci* (Thysanoptera: Thripidae). *Sci Data.* 2024;11(1):1003. <https://doi.org/10.1038/s41597-024-03737-8>
80. Zhang Q, Zhang Y, Wang J. Global gene expression in cotton fed upon by *Aphis gossypii* and *Acyrtosiphon gossypii* (Hemiptera: Aphididae). *J Entomol Sci.* 2023;58(1):47-68. <https://doi.org/10.18474/JES22-07>
81. Zhang J, Li J, Saeed S, Batchelor WD, Alariqi M, Meng Q, et al. Identification and functional analysis of lncRNA by CRISPR/Cas9 during the cotton response to sap-sucking insect infestation. *Front Plant Sci.* 2022;13:784511. <https://doi.org/10.3389/fpls.2022.784511>
82. Alagarsamy M, Amal TC, Karuppan S. Label-free quantitative proteomic analysis of the cotton (*Gossypium hirsutum* L.) genotypes with contrasting resistance to leafhopper (*Amrasca biguttula biguttula* Ishida). *bioRxiv*; 2023. <https://doi.org/10.21203/rs.3.rs-3041753/v1>
83. Venkatesulu S, Makula SP, Satihal MB, Puligundla SK, Srikanth K. Identification of SSR molecular markers for jassid resistance in cotton. *Agric Sci Dig.* 2023;43(5):695-700. <https://doi.org/10.18805/ag.d-5740>
84. Subhashini S, Keerthivarman K, Premalatha N, Kalaimagal T, Muthuswami M, Jeyakumar P. Molecular, cytological and morphological studies on jassid resistance in cotton (*Gossypium hirsutum* L.) based on hairiness trait. *J Cotton Res.* 2024;7(1):217. <https://doi.org/10.1186/s42397-025-00217-1>

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