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REVIEW ARTICLE

Advancements in cotton defoliation: From chemical harvest aids to genomic innovations

Selvamani Sanyasi[1], Ravikesavan Rajasekaran[2], Manikanda Boopathi Narayanan[3], Sakthivel Nalliappan[4], Kannan Nallathambi[5], Karthik Palanisamy[5] & Kumaresan Dharmalingam[1*]

[1]Department of Genetics and Plant Breeding, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[3]Department of Plant Biotechnology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[4]Agriculture Research Station, Tamil Nadu Agricultural University, Bhavanisagar 638 451, Tamil Nadu, India
[5]R&D Center, Rasi seeds Pvt. Ltd, Attur 636 141, Tamil Nadu, India

*Correspondence email - kumaresan.d@tnau.ac.in

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Abstract

Cotton is a crucial crop in the global textile market and its increasing demand necessitated the adoption of improved agronomic practices. Defoliation plays a vital role in enhancing harvesting efficiency and indirectly improves fibre quality by minimizing leaf trash contamination during mechanical harvest. This review critically examines the physiological, hormonal and molecular mechanisms governing defoliation in cotton, with particular focus on the roles of auxin, ethylene, abscisic acid and jasmonic acid in regulating leaf abscission. The complex interactions between these hormones influence the activation of the abscission zone and the efficiency of leaf drop. However, several challenges affect the performance of defoliants, including environmental variability, genetic differences among cultivars and the potential health and ecological risks associated with chemical defoliants. The differential response of cotton cultivars to defoliants complicates application strategies, often leading to inconsistent defoliation and increased production cost. To address these challenges, a multi-faceted approaches like deeper understanding of the molecular basis of defoliation, enhancement of defoliant efficacy and the development of cultivars with enhanced defoliant response are essential. This approach is supported by precision agriculture technologies, such as Unmanned Aerial Vehicle (UAV)-assisted spraying, optimized harvest-aid timing and dosage and strategic defoliant selection. Additionally, the identification of candidate genes and QTLs associated with defoliation response opens new opportunities for developing cultivars optimized for mechanical harvesting. This review stresses the need for integrated strategies that harmonize increased cotton production with ecological considerations. It calls for future research on sustainable practices, improved defoliation methods and the development of genotypes responsive to defoliants to enhance resilience in cotton cultivation.

Keywords: cotton; defoliation; harvest aids; mechanical harvest; transgenes

Introduction

Cotton (*Gossypium* spp.) is a prominent economic crop worldwide and serves as a main raw material for the textile industry. It is cultivated in more than 80 countries across various climatic zones and significantly contributes to economies and employment. Global cotton production levels fluctuate every year due to a combination of climatic variability, pest and disease pressures and policy or market dynamics. Major cotton-producing countries include China, India, the United States, Brazil and Pakistan. Recent estimates indicate that global cotton production is about 25-27 million metric tons each year and demand predominantly comes from the textile industry (1). The genus *Gossypium* comprises 46 diploid species and seven allotetraploid species, of which only four-*Gossypium arboreum*, *Gossypium herbaceum*, *Gossypium hirsutum* and *Gossypium barbadense* are cultivated for their spinnable lint, while the remaining species are wild types characterized by short seed fuzz (2). Among the cultivated species, *G. hirsutum* occupying about 90 % of the total cultivated area, followed by *G. barbadense* (8 %), whereas *G. arboreum* and *G. herbaceum* account for a minimal share globally (3).

The global cotton market was valued at USD 41.83 billion in 2023 and is projected to reach USD 53.64 billion by 2032, with a CAGR of 2.80 % from 2024 to 2032 (4). This growth is due to its major role in textiles, apparel, medicinal products and cottonseed oil. Asia-Pacific regions have key cotton-growing areas, particularly during 2023-24, China held the top spot in global production with 23.33 %, followed closely by India with 22.78 %. In terms of productivity, China recorded the highest yield at 2135.42 kg/ha, followed by Australia (2037.04 kg/ha), Brazil (1898.11 kg/ha) and Israel (1809.30 kg/ha) in 2024-25. Brazil led global exports with 12.39 million bales (27.32 %), followed by the United States (11.74 million bales, 25.88 %), Australia (5.47 million bales, 12.05 %) and India (2.11 million bales, 4.64 %) in 2023-24 (5). India's cotton exports increased from 1.589 million bales (USD 612 million) in 2022-23 to 2.84 million bales, generating USD 975 million in 2023-24, reflecting a growth of approximately 78.7 % in export volume and 59.3 % in export value (6). According to ICAC (2024-25), despite being the second-largest producer, India had the lowest productivity (440.52 kg/ha) among major cotton-growing countries, indicating the need for technological and agronomic improvements (5).

Defoliation plays a crucial role in modern cotton production, especially for mechanical harvesting (7). Traditional hand-picking is effective but labour-intensive and time-consuming. Rising labour costs and seasonal workforce shortages make this less practical (8). In contrast, mechanized harvesting offers a cost-effective and efficient alternative. Defoliation not only enhances harvesting efficiency but also reduces fiber contamination by minimizing the presence of leaf trash in harvested cotton. However, its success largely depends on the effective application of chemical defoliants (9). The effectiveness of defoliation is influenced by several factors, including crop maturity, environmental conditions, genotype variability and the proper selection and application of defoliants. Nevertheless, current cotton defoliation methods face limitations, such as inconsistent leaf drop, premature desiccation and environmental concerns associated with chemical usage (10). This review examines the importance of defoliation in cotton production and its significant impact on improving the efficiency of mechanical harvesting. It further examines the challenges of cotton defoliation methods and highlights recent advances in chemical, physiological and molecular approaches that improve defoliation efficiency. Additionally, it discusses the potential of emerging biotechnological tools and precision agriculture techniques to developing cost-effective defoliation solutions.

Defoliation mechanism in cotton

Defoliation in cotton is a controlled process involving enzymes and hormones. The application of defoliants initiates leaf abscission by triggering hormonal changes, primarily enhancing ethylene and abscisic acid (ABA) signaling. The abscission zone (AZ), a specialized layer of cells at the near base of the petiole, plays a key role in facilitating this process (11). Leaf abscission occurs in four distinct phases: determination of abscission cell fate, signal perception by AZ cells, activating detachment mechanisms and forming protective layer after post-abscission (12). A critical step is the degradation of intercellular and cell wall components. Pectin, a key component of the middle lamella, is hydrolyzed by enzymes such as pectin methylesterase, pectin polygalacturonase and pectin lyase. At the same time, the breakdown of the primary cell wall, composed of cellulose, hemicellulose and pectin, weakens the AZ structure. Enzymes such as polygalacturonase, cellulases, expansins and xyloglucan endoglycosidase/hydrolases work together to break down the cell wall matrix, allowing leaf to detach (13, 14). The efficiency of this enzymatic breakdown is influenced by hormonal regulation and environmental conditions, ensuring defoliation occurs at an optimal stage for plant productivity.

Hormonal regulation of defoliation

The hormonal regulation of defoliation in plants is a complex process that involves numerous plant hormones, including auxins, ethylene, cytokinins and abscisic acid (ABA). These hormones interact in a delicate manner to control leaf abscission, which can be triggered by environmental stresses, herbivory, or artificial defoliation (13, 15). Ethylene is the principal hormone driving defoliation, acting as a key signaling molecule in the abscission process. It upregulates the expression of genes encoding cell wall-degrading enzymes, such as *Cel1* and *Cel2* (cellulases) and *PG* (polygalacturonase), which hydrolyze cellulose and pectin in the leaf abscission zone, weakening the cell wall matrix and enabling leaf detachment (16). Experimental studies have shown that ethylene treatment increased *PG* expression by 3.5-fold and *Cel1* activity by 2.8-fold in the AZ, directly correlating with enhanced abscission rates (17). The transcription factors *EIN2* and *ERF1*, are key regulators of ethylene and it amplify abscission signaling by promoting downstream gene expression (18). These molecular changes facilitate the degradation of the middle lamella and primary cell wall, which are essential for cell separation and leaf shedding (19).

Auxin is crucial for defoliation, affects leaf abscission *via* multiple physiological and biochemical pathways. The "Auxin Gradient" theory states that an auxin concentration gradient across the AZ is key to abscission. High auxin levels at the distal end of the leaf inhibit abscission by maintaining cell integrity, while reduction in auxin promotes leaf shedding (20). Recent studies have shown that thidiazuron (TDZ) treatment leads to a 40-60 % reduction in auxin concentration in the abscission zone (AZ) of petiole base within 72 hr of application (21). This auxin reduction leads to downregulation of auxin-responsive genes such as *IAA1* and *AUX/IAA*, which normally suppress cell wall-degrading enzyme activity (22). Cytokinins also interact with ethylene and auxin in a complex hormonal network that regulates defoliation. Cytokinins, particularly zeatin, generally act as anti-senescence hormones, delaying abscission by maintaining chlorophyll stability and supporting nutrient mobilization. However, their reduction increases susceptibility to ethylene and facilitates leaf drop (21). Application of TDZ + diuron (200 ppm) reduced zeatin content by 32.7 %, which infer cytokinin suppression contributes to effective defoliant action in cotton (23). Cytokinins may also modulate AZ responses by altering ethylene sensitivity (24).

ABA promotes ethylene production by upregulating *ACS* (1-aminocyclopropane-1-carboxylate synthase) and *ACO1* (1-aminocyclopropane-1-carboxylate oxidase) genes, which increase ethylene levels by 2-3-fold under stress conditions (25). In defoliant-treated cotton plants (TDZ + diuron, 300 ppm), ABA levels were reported to increase by 48.6 %, further amplifying ethylene signaling (23). ABA also plays a vital role in ROS-mediated signaling pathways, indirectly facilitating abscission. Jasmonic acid (JA) accelerates senescence and can enhance ethylene production, particularly in response to wounding or pathogen attack. It upregulates genes involved in abscission zone activation (26). JA also play a major role in secondary abscission zone formation. It can act synergistically with indole-3-acetic acid (IAA) to induce changes related to abscission (27). These all-hormonal shifts elevate the levels of reactive oxygen species (ROS), particularly hydrogen peroxide (H_2O_2), which trigger oxidative signaling and activate cell wall-degrading enzymes. Excess ROS can cause significant cellular damage by degrading proteins, lipids and nucleic acids, compromising membrane integrity and promoting abscission. Application of TDZ + diuron (200 ppm) increased cellulase activity in leaves (62.4 %), petioles (68.6 %) and bolls (28.2 %), while 300 ppm led to a 95.1 % increase in petioles, confirming ROS-mediated enzymatic activation (23). Continuous H_2O_2 production, reduced antioxidant activity and IAA- and ABA-dependent signaling converge to induce abscission.

Significance of defoliation in cotton production

Cotton defoliation offers many advantages that significantly influences fiber quality, yield increase and harvest management (28). Defoliation of the lower canopy of the cotton plant is referred to as bottom defoliation. This practice was first used in the early 1960s (1963-1964) to modify the microclimate in cotton fields when conditions favored boll rot infestation (29). Bottom defoliation also improves ventilation and light penetration in the lower parts of the plant, reduces relative humidity and decreases the incidence of pests such as whiteflies, as well as diseases like *Ascochyta* blight, anthracnose and *Alternaria* leaf spot (30). Defoliation facilitates mechanical harvesting by ensuring uniform leaf drop, thereby minimizing leaf trash contamination and prevent fiber staining. This leads to clean lint with purity, improves ginning efficiency and market value (31). Defoliation in physiological perspective plays a vital role in optimizing source-to-sink dynamics. Defoliants are used to control excessive plant growth by causing leaf drop, then encourages the plant to shift photoassimilates towards reproductive parts to improve yields. These photoassimilates, primarily sugars produced through photosynthesis, are indeed transferred from vegetative tissues to developing bolls (30). A recent study shown that defoliation can increase single boll weight due to the efficient transfer of stored photoassimilates from cotton burs (31, 32). This practice also ensures synchronized boll opening by reducing the boll growth period by 3-6 days, minimize multiple harvest, save labour and production cost (33).

Harvest aids for defoliation

Defoliation is typically accomplished with a mixture of several chemicals collectively called harvest aids. The primary ingredients in harvest aids cause leaves to desiccate and fall from the plant. Additional ingredients may be added to cause mature bolls to open (boll openers), kill insects or weeds and prevent leaf regrowth (desiccants) (34). These aids facilitate harvest quickly, optimize productivity and preserve fiber quality by reducing leaf debris, preventing regrowth and minimizing weather-related losses. Defoliants facilitate leaf abscission by disrupting hormonal balance, primarily by increasing ethylene synthesis or inhibiting auxin activity (21). Thidiazuron, also known as N-phenyl-N-(1,2,3-thiadiazol-5-yl)urea, is a synthetic compound with cytokinin-like activity. It is one of the most effective defoliants, promotes leaf abscission by influencing the interplay of ethylene, auxin and abscisic acid (ABA), as well as affecting reactive oxygen species (ROS) metabolism and photosynthetic efficiency. Thidiazuron is particularly effective when applied at 60-80 % boll opening (35). Furthermore, the combination of thidiazuron and diuron promote cotton defoliation up to 98 % without increasing trash content in lint by reducing leaf growth and gas exchange characteristics in cotton (36). The next commonly used defoliant, tribufos, is an organophosphate compound, leading to controlled leaf senescence and drop (37). The effectiveness of defoliants depends on the timing and application rate. Excessive concentrations of defoliants can result in premature leaf desiccation, leading to "stuck" leaves that hinder mechanical harvesting. For instance, application of thidiazuron and diuron (commercially known as Ginstar®), at rates greater than the recommended dose of 189-473 mL per acre, can lead to stuck leaves under warm conditions (38). Desiccants, such as paraquat and sodium chlorate, accelerate the drying of leaves and stems and effectively terminating vegetative growth. Paraquat significantly affects plant height, leaf-area index and overall dry-matter accumulation and enhancing leaf fall percentage (39). However, paraquat application is generally restricted to cases where all mature bolls have opened and premature use can negatively affect fiber development (40). Boll openers, primarily ethephon, release ethylene to stimulate boll dehiscence, facilitates fiber exposure and enhance harvest efficiency. However, early application before boll maturity can adversely affect fiber quality like reducing micronaire and fiber length. Combining ethephon with defoliants enhances both boll opening and leaf drop, ensuring a more uniform and timely harvest (41). Thidiazuron-ethephon at high rates resulted in 90 % defoliation, 80 % boll opening and improved first harvest production without altering boll weight, lint percentage and fiber quality (42). A summary of harvest aid chemicals and their effects is presented in (Table 1).

Challenges in cotton defoliation

Cotton defoliation faces many challenges due to environmental factors, genetic differences, physiological complexities and economic constraints. The success of chemical defoliants depends on temperature, humidity and rainfall (43). The efficacy of defoliants is less in cold climates when temperature fall below 18 °C (44). In tropical and subtropical regions like India, high humidity and unpredictable weather cause uneven boll maturation, makes inconsistent defoliation and often require repeated applications. This increases production costs and prolonging the harvest leads to deterioration of fiber quality. Additionally, the variability in defoliation response among different cotton cultivars complicates large-scale implementation. Some cultivars respond well to defoliants but others resist them making it difficult to establish a standard defoliation method. The lack of extensive research on diverse cotton germplasm restricts breeding machine-harvest-friendly cultivars with better defoliation traits (45).

Another major challenge in cotton defoliation is post-defoliation regrowth, arises due to perennial and indeterminate growth habit of cotton. When the bolls attain maturity, they stop absorbing nutrients, excess photosynthates accumulate and this often leads to a second flush of vegetative growth, referred to as regrowth. This regrowth negatively affects fiber quality and increases trash content to more than 10-12 % in harvested cotton. It also leads to the accumulation of plant debris, provides a suitable habitat for insect pests and fungal pathogens (46). For example, the southern root-knot nematode (*Meloidogyne incognita*) is a damaging parasite of cotton that, in combination with cotton regrowth, causes significant economic

Table 1. Harvest aid chemicals and their effects in cotton defoliation

Harvest aid chemical	Effects	Reference
Carfentrazone-ethyl	Defoliates and desiccates leaves; requires adjuvants for efficacy	(85)
Carfentrazone-ethyl + fluthiacet-methyl	Defoliates and desiccates leaves	(86)
Cyclanilide	Enhances boll opening and defoliates when mixed with ethephon	(39)
Dimethipin	Defoliates leaves	(82)
Endothall	Hastens defoliation/desiccation in tank mixes; toxic to fish	(66)
Ethephon	Stimulates boll opening and maturation; may cause defoliation at higher rates; can reduce fiber quality if applied early	(87)
Ethephon + AMADS	Improves defoliation, particularly for cutout cotton; limited regrowth control	(39)
Ethephon + Cyclanilide	Improves defoliation, provides some regrowth control	(88)
Ethephon + Dimethipin	Enhances defoliation and boll opening, effective in cooler climates	(39)
Ethephon + Thidiazuron	Accelerates boll opening and leaf drop, improves early harvest	(42)
Ethephon + urea sulfate	Combines effects of ethephon; exact effects may vary	(89)
Glyphosate	Suppresses regrowth, controls late weeds; do not use on Roundup Ready cotton	(90)
Paraquat	Desiccate leaves rapidly; may stick them; helps open mature bolls	(51)
Pyraflufen ethyl	Defoliate and desiccate leaves; requires adjuvants for efficacy	(88)
Saflufenacil	Defoliate and desiccate leaves; requires specific adjuvants	(91)
Sodium chlorate	Can act as defoliant or desiccant depending on rate and timing; low cost, low mammalian toxicity	(85)
Thidiazuron	Defoliate leaves, controls regrowth and remove younger leaves	(42)
Thidiazuron + Diuron	Defoliate leaves, improves efficacy, controls regrowth; can desiccate/stick leaves at high rates	(39)
Tribufos	Defoliate mature leaves; poor regrowth control	(92)

losses. In 2016, losses due to the southern root-knot nematode across the United States Cotton Belt were estimated at 2.2 %, equivalent to approximately 414700 cotton bales (47). Managing regrowth requires additional chemical applications, further increasing production costs and environmental risks. From a physiological perspective, defoliation is a complex process that involves many hormonal pathways, such as cytokinin, ethylene and auxin, as well as reactive oxygen species (ROS) metabolism (21). The interaction between these regulatory mechanisms affects the rate and efficiency of leaf abscission and the basic genetic architecture remains unexplored (20). The extensive use of herbicidal-based chemicals such as tribufos, glyphosate and paraquat poses potential risks to both the environment and human health (48). Repeated applications can contaminate soil and water, disrupt microbial ecosystems and pose health hazards to farmworkers and nearby communities. Improper application may also result in spray drift, negatively affecting non-target crops and native biodiversity.

Strategies to enhance cotton defoliation

Enhancing cotton defoliation requires a combination of optimized application timing, improved defoliant formulations and advanced spraying technologies. Precision approaches such as crop age-based harvest aid application, Unmanned Aerial Vehicle (UAV)-assisted spraying and optimizing droplet size of defoliants significantly improve efficiency. Breeding defoliation-efficient cultivars with desirable physiological traits can enhance uniformity and reduce repeated applications (Fig. 1).

Crop maturity-based harvest aid application

Conventional defoliant application methods depend on variables such as weather, field conditions and crop growth stages. As a result, they often lead to inconsistent harvest schedules and reduced harvesting efficiency. Crop maturity-based applications offer a systematic method by taking into account plant maturity, which enhances resource efficiency (49). The timing of harvest aid application in cotton is determined by several methods. These include assessing the cotton boll opening rate, calculating the effective accumulated temperature, counting the number of main stem nodes above the first cracked boll, using the knife cutting method and predicting micronaire values. Among these, the most widely used methods are the node above cracked boll (NACB) method and the boll opening rate. These methods, provide reliable indicator of crop maturity and readiness for defoliation (43). Defoliation at 40 % boll opening stage using thidiazuron and diuron had no adverse effects on yield and fiber quality, making it a viable approach for mechanical harvesting in the variety Maras in Southeast Anatolia, Turkey (50). Application of 1500 ppm paraquat at 150 days after sowing (DAS) resulted in the highest defoliation, while ethrel at 2500 ppm (also at 150 DAS) produced the maximum boll weight, seed cotton yield and net revenue in the rainfed cotton variety *SVPR2* (51). However, these results are specific to this variety and its growing conditions and may not be directly applicable to other cotton cultivars. Similarly, the application of Dropp Ultra® (240 g/L thidiazuron

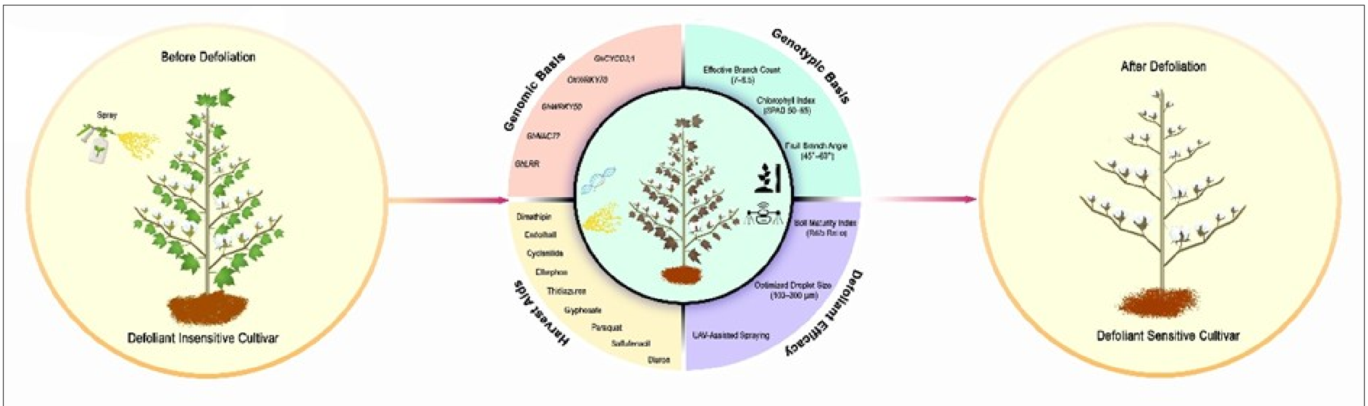

Fig. 1. A diagrammatic illustration of strategies to enhance defoliation in cotton.

120 g/L diuron) on Lima and Candia cultivars showed that sowing at the right time significantly improved yield.

Defoliation at 60 % boll opening further increased the number of open bolls and seed cotton weight. However, these benefits can vary across cultivars and environmental conditions (52). Application of 200 mL/ha of Dropp Ultra® at 150 DAS balanced vegetative and reproductive growth effectively in the cotton cultivars MRC 7361 BGII and MRC 7017 BGII. Whereas higher doses at 225 mL/ha had a negative impact in yield (53). Application of defoliant improved defoliation (94.6 %) and boll opening (85.4 %). However, responses varied by cultivars (42), L7619 exhibited the highest defoliation rate (95.6 %), but it faced significant yield reduction (882.9 kg/ha). Late spraying achieved the highest defoliation (97.3 %), boll opening (89.8 %) and seed cotton yield (3991 kg/ha) and increase fiber strength (0.59 cN/tex). Additionally, cotton bolls with an age of less than 37 days are vulnerable, showed reduced boll weight and compromise fiber quality (54). In some instances, delayed defoliation may expose plants to unfavourable weather conditions, potentially leading to a decline in fiber quality. The ratio of boll age to boll period (Rd/b) is considered as an important criterion to further refine the harvest aid application. This method accounts for cotton varietal differences and their morphological characteristics, addresses the limitations of boll opening rate method. To find best spraying time by using Rd/b helps balance between boll weight and fiber quality (33). This method provides a theoretical framework for synchronizing boll weight improvement and fiber quality, particularly for machine-harvested cotton.

Enhancing efficacy of defoliants

The strategic methods of defoliation application can improve defoliation efficiency. Recent innovations, such as UAV or drone-based precision spraying, have significantly improved defoliation efficiency in cotton. UAV or drone-based precision spraying is the breakthrough. It allows precision defoliant application, reduces chemical loss and ensures uniform distribution across the field, less drift and faster application across broad regions, particularly in tough terrains. Additionally, drone spraying eliminates manpower dependency, making it an efficient alternative to manual or tractor-based applications. UAV-based defoliant application can boost defoliation efficiency by 5-10 % and reducing chemical use by up to 30 % when compared to conventional spraying methods (55, 56). Another important element in enhancing the effectiveness of defoliants is optimizing the size and deposition of spray droplets. Droplet size, coverage and absorption have a significant impact on defoliation efficacy. The use of fine to medium droplet sizes (100 -300 µm) guarantees improved adherence and penetration of the leaves. Adjuvants and surfactants are used to boost defoliant uptake and electrostatic spraying technology lowers drift and waste by improving droplet attraction to leaf surfaces. The defoliation efficiency can be increased by 10-15 % by optimizing droplet size and surfactant-enhanced formulations (57). The integration of smart sensor-based spraying enables the real-time modifications in defoliant application based on crop condition, canopy density and leaf senescence. Multi-spectral imaging sensors monitor plant stress levels, while AI-driven Variable Rate Technology (VRT) adjusts the defoliant dosage according to crop maturity (58). GPS-controlled site-specific application avoid wastages of chemical use, minimizing environmental impact and enhance efficiency. Smart sprayers using AI-controlled dosage have led to a 20 % reduction in defoliant consumption while preserving yield and fiber quality (59, 60). Overall, these advanced approaches reduce chemical waste, increase yield and enhance the overall effectiveness of cotton defoliation are important for modern cotton farming.

Enhancing efficacy of defoliants under low temperature: During low-temperature conditions, the efficiency of defoliants often fell short of meeting the requirements for machine-picked cotton (44). Therefore, enhancing defoliation efficacy under low temperatures is crucial. The combined application of thidiazuron (TDZ) and cyclanilide (CYC) can significantly improve defoliation at daily mean temperatures of 15 °C (17/13 °C). It enhances cotton defoliation under low temperature by modulating hormone pathways and reactive oxygen species (ROS) systems. Specifically, it regulates genes involved in auxin, ethylene and jasmonic acid biosynthesis and their transport and signaling processes, thereby influencing ROS homeostasis (7). In cotton, the combined application of thidiazuron (TDZ) and cyclanilide (CYC) at low temperatures downregulates auxin biosynthesis (*TAA*) and response-related genes (*ARF*, *AUX1*, *IAA*), leading to reduced auxin content during the early stages of abscission (61). This auxin depletion establishes a gradient in the abscission zone (AZ), creating hormonal imbalance that enhances ethylene sensitivity. Concurrently, TDZ+CYC treatment upregulates ethylene response factor (*ERF*) genes and increases ethylene content in AZs, promoting pectin degradation and accelerating leaf separation (62). In addition, moderate upregulation of jasmonic acid (JA) biosynthesis genes (*AOC4*, *OPR*) and signaling components (*JAR1*, *COI1*, *MYC*, *JAZ*) contributes to cell wall polysaccharide degradation, facilitating abscission (7). Notably, the upregulation of *JAR1*, *MYC* and *COI1* enhances JA-mediated cell wall hydrolase activity, reinforcing defoliant effectiveness (63). Furthermore, TDZ+CYC significantly upregulates *RBOH* genes at later stages (144 hr), resulting in elevated levels of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in AZs. H_2O_2, a key regulator of ROS homeostasis, acts as a signaling molecule that modulates the expression of cell wall-degrading enzymes such as polygalacturonases (*PG*) (64). The early activation of *PG* genes by TDZ+CYC, along with ROS accumulation, indicates that H_2O_2 function as a secondary messenger that enhances cell wall loosening and drives the abscission process. Collectively, these molecular responses illustrate that TDZ+CYC-mediated defoliation in cotton involves coordinated regulation of hormone signaling and ROS pathways, particularly under low-temperature conditions (7).

Breeding defoliation-efficient cotton cultivars

Cotton cultivars play a crucial role in determining the effectiveness of defoliants, making their sensitivity to defoliation as an important factor in improving harvesting efficiency. Cotton cultivars that are highly responsive to defoliants tend to grow rapidly, exhibit a high boll opening rate, demonstrate effective defoliation and ultimately maintain high net production rates with minimal quality loss during mechanical harvesting (65). Although some cultivars are inherently sensitive to defoliant chemicals, their productivity under defoliant treatment depends on careful monitoring of temperature regimes, plant water status and synchronization of boll bursting with the appropriate growth stage. Recent studies indicate that suboptimal environmental conditions can amplify the stress induced by defoliants, resulting in leaf scorching, premature abscission and boll injury (66). Compact cotton genotypes, characterized by short branches and sparse, deeply lobed leaves, exhibit higher responsiveness to defoliants compared to long-branch and dense-canopy types. These traits facilitate better penetration and action of defoliants, resulting in more efficient leaf abscission and improving harvest readiness. In contrast, genotypes with large, dense foliage or excessive vegetative growth, often induced by high nitrogen levels, show reduced sensitivity to defoliants. Therefore, developing compact plant types with optimized canopy architecture is a strategic approach to enhance defoliation efficiency under mechanical harvesting systems (30). Identifying such breeding materials through traditional field-based phenotyping methods has been challenging due to the manual and time consuming. This has created bottlenecks in connecting genotype to phenotype and limiting crop improvement efforts (67). The development of high-throughput phenotyping (HTP) for cotton defoliation marks a big step forward in breeding programs by using mechanized harvesting and defoliation studies. HTP platforms, particularly those incorporating UAVs, offer a scalable and cost-effective solution for large-scale field phenotyping (68). UAVs equipped with advanced cameras and sensors can capture high-resolution field imagery, allowing automated assessments of key cotton traits. Recent advancements in cotton phenotyping includes counting the number of bolls through ground robot system (69), measuring plant height and canopy cover through multispectral imaging (70), counting number of flowers using aerial imaging (71) and estimating water status with thermal imaging (72).

For defoliation-specific phenotyping, the important agronomic traits such as number of effective branches per plant (7-8.5), chlorophyll SPAD values (50-65), fruit branch angle (45°-60°) and hanging rate exhibit strong correlations with defoliation efficiency (65). However, a key challenge in using SPAD readings to predict defoliation outcomes lies in their sensitivity to chemical treatments. Studies evaluating various defoliants, including ethephon, sodium chlorate and thidiazuron plus diuron combinations, have shown that these chemicals significantly influence SPAD values, as well as defoliation percentages and boll opening rates. Although defoliant applications consistently affect SPAD measurements, the relationship between altered SPAD values and actual defoliation success remains complex and highly dependent on the specific treatment used (73). This suggests that monitoring of chlorophyll content through imaging or SPAD meters could be instrumental in evaluating defoliation-related traits. UAVs improve phenotyping further by facilitating precise application of defoliant and enabling the collection of large-scale data across extensive experimental plots. Moreover, monitoring the persistence of “dead but not falling” leaves, or hanging rates, provides valuable insights into defoliation efficiency. By integrating these agronomic traits with imaging technologies and machine learning, HTP systems can accurately quantify defoliation characteristics, ultimately accelerating the breeding and selection of cotton varieties optimized for mechanized harvesting. This approach not only improves the efficiency of defoliation strategies but also enhances the overall productivity and fiber quality of cotton crop.

Expression of defoliation-associated genes

Understanding key genes regulating defoliation is essential for optimizing leaf shedding in cotton and critical factor for improving the efficiency of mechanical harvesting (74). A Phylogenetic study classified somatic embryogenesis receptor-like kinase (*SERK*) genes into three subfamilies, suggesting shared biological activities. Expression profiling after defoliant treatment in *G. hirsutum,* indicated that necessary component of brassinosteroid signaling (*GhSERK2-2*), was markedly upregulated, facilitating leaf abscission. Conversely, suppression of *GhSERK2-2* reduced defoliation, underscoring its regulatory role in abscission signaling. In addition to SERK-mediated pathways, RNA-seq analysis identified 13764 differentially expressed genes (DEGs) in response to thidiazuron (TDZ) treatment. Many of these genes are involved in auxin transport and signaling. Among them, the auxin transporter *GhPIN3a* was shown to be essential for TDZ-induced abscission. Its overexpression in *pro35S:GhPIN3a:YFP* transgenic plants resulted in reduced defoliation, suggesting that *GhPIN3a* maintains auxin gradients that delay abscission. Furthermore, co-expression network analysis uncovered five key transcription factors, such as, *GhNAC72*, *GhWRKY51*, *GhWRKY70*, *GhWRKY50* and *GhHSF24* that likely coordinate TDZ-induced transcriptional reprogramming during abscission (74). Genotypic variation also plays a critical role in defoliant sensitivity. For instance, cultivar X50 (defoliant-sensitive) and X33 (defoliant-insensitive) displayed distinct transcriptomic profiles, with RNA-seq identifying 2434 DEGs, particularly within cytokinin and ethylene signaling pathways. Notably, *GhCKX3* (cytokinin oxidase/dehydrogenase) was highly upregulated in X50 following treatment with TDZ and ethephon. This upregulation promoted ethylene biosynthesis while reducing cytokinin levels. Functional validation revealed that *GhCKX3* modulates defoliation by influencing ethylene responsiveness and delaying leaf abscission, thus confirming its key role in the hormonal regulation of leaf shedding (20). These findings underscore the intricate hormonal and genetic regulation underlying defoliation in cotton, offering targets for breeding cultivars optimized for chemical defoliation and mechanical harvesting.

Genomic basis of defoliation in cotton

The genomic basis of defoliation in cotton involves complex factors that affect leaf-shedding process in cotton plants. This process is important for both effective harvesting and environmental adaptation. Defoliation in cotton is governed by genetic differences that influence hormone signaling, transcription factors and cell wall breakdown mechanisms. Ethylene is the principal hormone regulating leaf abscission and alterations in its production genes (*ACS*, *ACO*) and receptors (*ETR*, *EIN2*) affect defoliation sensitivity (44). Genes involved in auxin transport (PIN, AUX1) and auxin response factors (ARFs) are essential for leaf retention and abscission (75). Moreover, abscisic acid (ABA)-responsive genes govern stress-induced leaf abscission, especially during drought, whereas brassinosteroids (BRs) signaling *via GhBZR1* influences leaf senescence and abscission (76).

Transcription factors (TFs) govern gene expression associated with cell separation at the abscission zone. NAC TFs (*GhNAC072*, *GhNAP1*) regulate senescence and abscission through the modulation of cell wall degradation genes. Whereas WRKY TFs (*GhWRKY50*, *GhWRKY70*) affect stress responses and pathways associated with abscission (77, 78). Similarly, MYB TFs (*GhMYB108*) assist in secondary cell wall remodelling, altering leaf detachment and HD-ZIP TFs (*GhHB25*) regulate hormone signaling in the abscission zone (79, 80). The genetic differences in cell wall-modifying enzymes influence the ease of leaf abscission. Pectin-degrading enzymes, including *GhPG* (polygalacturonase) and *GhPME* (pectin methyl esterase), decompose the middle lamella in the abscission zone. The cellulose and hemicellulose modifiers, such as expansins (EXPA1, EXPA5) and β-1,4-glucanases, facilitate cell separation. Furthermore, GhCAD (cinnamyl alcohol dehydrogenase), a critical gene in lignin production, may alter abscission zone strength by modulating lignin deposition and tissue rigidity. While its direct function in AZ development in cotton has to be experimentally established, differential expression and allelic variation of *GhCAD* have been related to defoliation sensitivity in prior investigations (81, 82). Recent genomic studies, including those by Li et al. (45), have identified key loci and candidate genes regulating defoliation. Genome-wide association studies (GWAS) pinpointed two major loci-RDR7 (chromosome A02) and RDR13 (chromosome A13)-that influence relative defoliation rate (RDR). Candidate genes such as *GhLRR* (*GhA02G015900*) and *GhCYCD3;1* (*Gh_A13G042700*) play vital roles in leaf abscission by affecting protein function and cell cycle regulation. Functional validation confirmed that defoliant treatments like TDZ enhance their expression, while gene silencing reduces defoliation rates, proving their direct involvement in defoliation efficiency.

Recent research has identified two quantitative trait loci (QTLs), *qDS-A05* and *qDS-A06*, linked to defoliation, discovered by GWAS. Among these, *qDS-A06* reliably affected leaf abscission across several conditions. The major gene within this region, *GhDS-A06*, encodes a carboxylate clamp (CC)-tetratricopeptide repeat (TPR) protein, which plays a regulatory function in abscission zone development. This protein is thought to engage with components of the auxin and ethylene signaling pathways and may modulate the expression of cell wall-degrading enzymes, including cellulases and polygalacturonases, which are crucial for organ separation. Haplotype analysis suggests that the favorable *GhDS-A06* allele has been artificially selected in northern China, improving adaptation to machine-harvested cotton (14). Table 2 illustrates the overview of loci and associated genes contributing to defoliation processes. These discoveries provide molecular targets for breeding efforts aimed at improving defoliation efficiency through gene editing technologies like CRISPR and marker-assisted selection (MAS) (83). By integrating genomic insights, hormone regulation and transcriptional control, breeding programs can develop cotton varieties with improved defoliation responses. Improving genetic features for increased defoliant sensitivity in cotton presents the opportunity to decrease chemical usage, minimize environmental effects and enhance harvesting efficacy. This strategy requires meticulous management (30). Inadequate calibration may result in excessive defoliation, leaf scorch and boll damage, particularly under specific weather conditions due to increased sensitivity (84). These dangers underscore the necessity for a comprehensive study of the physiological reactions to defoliants and the environmental elements that affect them. An equitable, precision-oriented defoliation approach that accounts for varietal sensitivity and environmental variability is crucial for enhancing crop quality, harvestability and sustainability in current cotton production.

Table 2. QTLs and candidate genes regulating defoliation in cotton

QTL	Chromosome	Associated trait	Candidate gene	Gene function	Reference
RDR7	A02	Relative defoliation rate	*GhLRR*	Leucine-rich repeat protein; regulates leaf abscission	(45)
RDR13	A13	Relative defoliation rate	*GhCYCD3;1*	Cyclin D3-type protein; involved in cell cycle regulation and defoliation timing	(14)
qDef-A11	A11	Leaf shedding	*GhNAC72*	NAC transcription factor; associated with senescence and abscission	(83)
qDef-D03	D03	Defoliation response	*GhWRKY70*	WRKY transcription factor; modulates stress responses and leaf abscission	(74)
qDef-D05	D05	Sensitivity to defoliants	*GhWRKY50*	WRKY transcription factor; influences abscission-related pathways	(74)

Conclusion

This review highlights the important role of defoliation in improving cotton production and making mechanical harvesting more efficient. These factors are crucial for meeting the increasing global demand for cotton amid economic and environmental challenges. By exploring the physiological and molecular process of defoliation, this review lays groundwork for better understanding of the defoliant practices through innovative biotechnical and precision agriculture methods. However, while the vision of reducing chemical defoliants is commendable, it remains impractical for large-scale commercial cotton farming at present. Most mechanized harvesting systems still heavily rely on chemical defoliants for operational efficiency and existing genetic solutions are not yet sufficient replacements. Although several genes have been identified as promising candidates for enhancing defoliation sensitivity through gene editing, the technology is still in early developmental stages. No gene-edited cultivars have yet been widely adopted that can reliably minimize yield losses solely through modified defoliation responses. Additionally, challenges such as genetic heterogeneity among cotton varieties and the environmental impact of chemical defoliants continue to pose obstacles. Future research should therefore aim at developing integrated, eco-friendly defoliation systems that combine improved genetic strategies with reduced reliance on chemical defoliants. Advancements in HTP and precision agriculture techniques offer promising avenues toward achieving these goals. Interdisciplinary collaboration among agronomists, biotechnologists, plant breeders and environmental scientists will be essential in developing robust, scalable technologies that balance productivity and sustainability in the cotton industry.

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Authors' contributions

SS has done conceptualization, literature review and prepared initial draft of the manuscript; KD and RR given suggestions and carried out the final editing of the manuscript; MBN, SN, KN and KP helped in proofread the manuscript.

Compliance with ethical standards

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