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REVIEW ARTICLE

Thidiazuron as a defoliant to facilitate mechanical harvesting in cotton: A comprehensive review

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Abstract
Cotton is primarily cultivated for its commercial fiber, which plays a significant role in India's agro-industrial sector. It is one of the primary raw materials for producing feed, oil, fiber, and biofuel. Currently, farmers in India widely employ machine harvesters to harvest cotton. However, excessive leaf vegetation poses challenges in boll picking, adversely affecting fiber quality and reducing mechanical harvesting efficiency. Various chemical defoliants are applied to remove leaves before harvesting to address this issue. These defoliants promote leaf shedding, minimize debris in the cotton, and enhance boll opening and picking efficiency. Thidiazuron is a potent hormonal defoliant used in cotton to induce defoliation by increasing ethylene production while inhibiting the synthesis and transport of auxins. Notably, it interferes with the crosstalk between the phytohormones, such as cytokinin and ethylene, which regulates cotton defoliation. The method and timing of defoliant application are crucial for improving cotton harvesting efficiency. This review aims to provide a clear understanding of thidiazuron's application in synchronizing harvests, ultimately supporting the mechanization of cotton harvesting.

Keywords
cotton; defoliants; phytohormones; thidiazuron

Introduction
Cotton (*Gossypium spp.*), often called the " king of fiber," is vital in generating agricultural income, boosting export revenue, and creating employment opportunities. It significantly contributes to global agriculture and industry development (1). Annually, around 25 million metric tonnes of cotton are produced worldwide. As the largest cotton producer, India contributes approximately 26% of the world's cotton production despite having a relatively low yield per hectare (2). For the 2023-2024 marketing year, India's production is expected to reach 5.66 million metric tonnes, with 12.7 million hectares under cultivation (3). Cotton is often called "white gold" due to its economic significance, as it generates substantial profits for farmers.

Despite its importance, cotton production faces various global challenges, including erratic weather patterns, soil degradation, weed pressure, pest and disease outbreaks, and the rise of herbicide-resistant weeds (4). Improving cotton yield, productivity, and quality relies heavily on adopting advanced technologies, particularly in harvesting. The growth of cotton is unpredictable, with bolls maturing at different times and opening late, which can cause labor shortages during harvest. Additionally, the lint quality of late-opening bolls is typically inferior. As a result, cotton harvesting is often labor-intensive, expensive, and time-consuming (5). Mechanized picking can address these challenges in cotton farming by reducing harvesting costs and ensuring timely crop collection (6). Successful mechanical harvesting requires the availability of suitable cotton cultivars, growth hormones, regrowth inhibitors, defoliants, and desiccants (7).

Defoliation promotes the early and uniform opening of cotton bolls, reducing trash in seed cotton, preventing dead leaves from contaminating the cotton lint, and improving both cotton quality and yield. These benefits enhance the overall efficiency of cotton harvesting (8). Defoliants are chemicals that encourage leaf drop, thereby minimizing leaf contamination in harvested cotton fiber and improving picking efficiency. Additionally, defoliants help synchronize the boll-opening process in cotton (9). Among the various defoliants used in cotton production, thidiazuron is particularly effective. It works by creating an abscission zone at the base of the petiole, facilitating leaf drop. Abscission is triggered by signals from the distal parts of plant organs, though the exact mechanism remains unclear. Thidiazuron primarily influences plant hormones, specifically auxins, ethylene, which regulate the process of leaf abscission. Notably, thidiazuron induces cotton leaves to produce large amounts of ethylene, which plays a crucial role in defoliation. However, the efficacy of thidiazuron depends on factors such as crop stage, application method, timing, and the concentration of the defoliant (10). This review explains thidiazuron's role, its effect on abscission zone formation, phytohormone activity, and the optimal application methods. The insights provided will contribute to optimizing thidiazuron use, ensuring effective defoliation, maintaining fiber quality, and maximizing efficiency in mechanical harvesting (11).

Thidiazuron and its role as a defoliant

Thidiazuron, also known as N-phenyl-N-(1, 2, 3-thidiazol-5-yl) urea, is a synthetic cytokinin-like compound that stimulates the production of hormones such as ethylene and abscisic acid, as well as hydrolytic enzymes that break down cell walls (12). When applied in combination with diuron [3-(3,4-Dichlorophenyl) 1,1-dimethylurea], it inhibits photosynthetic electron transport, which significantly impacts juvenile leaves by promoting abscission while preventing regeneration (13). Higher doses of diuron and thidiazuron lead to extended periods of regrowth inhibition (14). Thidiazuron plays a crucial role in sustainable cotton production as a defoliant (15). While defoliants do not directly affect boll ripening, their use with a boll opener, such as ethrel, ensures effective defoliation and boll opening (16). Applying thidiazuron alongside ethrel results in a higher defoliation rate and faster boll opening within seven days (17). However, weather conditions and canopy density greatly influence the efficiency of defoliation and boll opening. The effectiveness of thidiazuron depends on timing, dosage, temperature, and the condition of the cotton plants (18). Table 1 displays different dosages of thidiazuron utilized for cotton defoliation.

Table 1. The effect of thidiazuron on cotton defoliation

Dosage	Effects	References
500 g ha^{-1} (0.1%)	Loss of leaf water content at 3rd day. Increased H_2O_2 content to 66% within 3 days after spraying.	(11, 19)
	Abscission zone formation within 4 days after spraying	
	Decreased the photosynthetic rate, transpiration rate and stomatal conductance within 3 days	

Mechanism of abscission zone formation

Abscission zones (AZs) are small, dense cells connected by plasmodesmata, which form only after the initiation of abscission and are responsible for the separation of plant organs (19, 20). The development and regulation of AZs in plants involve a complex physiological process. The development of AZ is induced by the activation of particular genes and the differentiation of cells in a localized area at the base of the leaf or organ. This process is regulated by several signals, with hormone signals playing a pivotal role. Among these, signals related to auxin and ethylene are very significant in modulating the abscission process.

The formation of AZs is shaped by the levels of endogenous auxin, particularly indole-3-acetic acid (IAA), which typically inhibits abscission by promoting cell adhesion and blocking the activation of genes related to cell separation. Higher auxin levels at the abaxial region inhibit the formation, positioning, and size of the AZ. Changes in auxin transport can alter its distribution across the leaf, triggering cell activation or differentiation within the AZ (21). While auxin plays a primary role, its effect is concentration-dependent and is modulated by ethylene and abscisic acid, which help shape the auxin gradient (11).

Thidiazuron primarily stimulates the activity of the IAA-oxidase system, reducing auxin concentration by inhibiting its transport, thereby promoting abscission. Ethylene also plays a key role by enhancing the production of cell wall-degrading enzymes (CWDEs) such as pectinase, polygalactosidase, and cellulose (22). These enzymes weaken and degrade the cell walls and the middle lamella, leading to cell separation and organ shedding. Increased peroxidase activity has also been linked to abscission, particularly in forming the abscission layer (23, 24). Abscisic acid further accelerates the senescence process by inducing ethylene production, inhibiting auxin transport, and increasing cellulase activity. For instance, during defoliation, defoliants like thidiazuron disrupt the normal role of auxin by inhibiting its synthesis or transport, causing a hormonal imbalance in the plant (25). The reduced auxin levels in the AZ activate enzymes such as cellulase and polygalacturonase, which hydrolyze cell walls and weaken cell adhesion, thus promoting leaf abscission.

Thidiazuron induces cotton leaf abscission zone formation

Thidiazuron has garnered significant attention for its ability to induce cotton leaf abscission effectively. It facilitates the natural separation of leaves from the stem upon absorption, making it a highly efficient defoliant. Numerous studies have explored the mechanisms of plant abscission, particularly under environmental stress (26, 27). Common side effects of this process include reduced chlorophyll content and changes in leaf water potential (28). Additionally, the excessive production of reactive oxygen species (ROS) plays a crucial role in activating cell wall-degrading enzymes (CWDEs), which contribute to cell wall digestion and leaf abscission (Fig. 1).

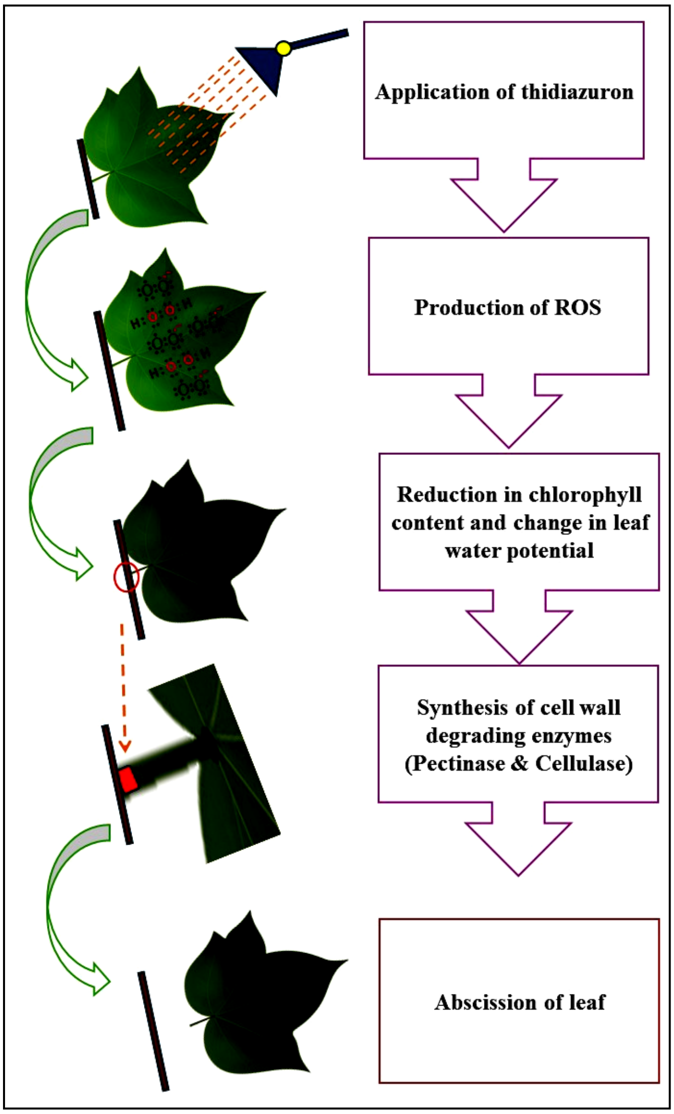

Fig. 1. Effect of thidiazuron application in the leaf abscission of cotton. Thidiazuron application produces excess reactive oxygen species (ROS), lowering the chlorophyll content, leaf water potential, and stimulating the cell wall degrading enzymes such as cellulase and pectinase, ultimately causing leaf abscission in cotton.

Research has shown that ROS-triggered asymmetrical programmed cell death (PCD) at the abscission zone (AZ) is one of the main factors regulating leaf abscission (29). There is a well-established correlation between ROS and the regulation of leaf shedding in plants. In cotton, thidiazuron induces leaf abscission by promoting the accumulation of hydrogen peroxide (H_2O_2) at the AZ, a common ROS involved in cell death and AZ formation. The production of H_2O_2, mediated by respiratory burst oxidase homologs (RBOH), has been identified as a key factor in thidiazuron-induced leaf abscission (27).

Thidiazuron promotes gene expression of auxin synthesis and signaling in cotton

Phytohormones such as ethylene, auxin, and cytokinins play a crucial role in regulating the process of leaf abscission in plants, as is well established (30). Ethylene, a gaseous hormone, is involved in several plant functions, including flower abscission and leaf senescence. Its interaction with other hormones, like auxin, further influences leaf abscission (31). Cytokinins, on the other hand, regulate both leaf growth and abscission. Through their complex interactions, phytohormones govern the intricate process of leaf abscission. For instance, thidiazuron, which mimics cytokinin activity, stimulates ethylene production and alters the cytokinin balance. This leads to changes in endogenous hormone levels, ultimately inducing leaf abscission and promoting boll opening (32).

Indole-3-acetic acid (IAA), the principal auxin in higher plants, is crucial in plant growth and development and is synthesized from the amino acid tryptophan (Trp) (33, 34). Auxin, particularly IAA, is essential for coordinating several growth processes in plants, including leaf retention and attachment, by inhibiting the activation of the abscission zone (AZ), which is vital for overall plant development. High levels of auxin generally prevent the activation of enzymes that facilitate cell separation in the AZ, thus promoting leaf retention. Conversely, lower levels of IAA in the older parts of the plant trigger AZ development, leading to leaf abscission. Therefore, auxin concentration gradients regulate AZ formation, and the position and size of the AZ are determined by auxin transport and signaling pathways (20). Thidiazuron disrupts the typical function of auxin in cotton plants, leading to defoliation by inhibiting auxin synthesis or transport within the plant. This disruption promotes AZ activation, causing leaf detachment and shedding (19). Ethylene also plays a significant role in the defoliation process triggered by auxin (35). Auxin-response genes, such as *Aux*/IAA, Small Auxin Upregulated RNAs (*SAUR*), Gretchen Hagen 3 (GH3), and Auxin Response Factors (*ARF*s), are critical elements in auxin signaling. The abscission process, which converts active free IAA into an inactive conjugated form, is mediated by *ARF* and *GH3* genes. These genes are potential targets through which thidiazuron promotes leaf abscission and reduces IAA content in cotton leaves. Auxin transporter genes also play an essential role in thidiazuron-induced leaf abscission by precisely controlling auxin transport (20). Molecular investigations have confirmed that thidiazuron application in cotton affects the expression of 68 genes linked to auxin signaling. These include eight *ARF*s, four *GH3* proteins, thirteen *SAUR* family proteins, nine genes encoding transport inhibitor response 1 (TIR1), twenty-nine *AUX*/IAA genes, and two genes for the auxin influx carrier (*AUX*1), all of which were downregulated within 24 hours of thidiazuron treatment (36). Additionally, thidiazuron can affect auxin transport by downregulating key auxin signaling components like AUX and tryptophan transport proteins (*TRP* 1) (20) (Fig. 2).

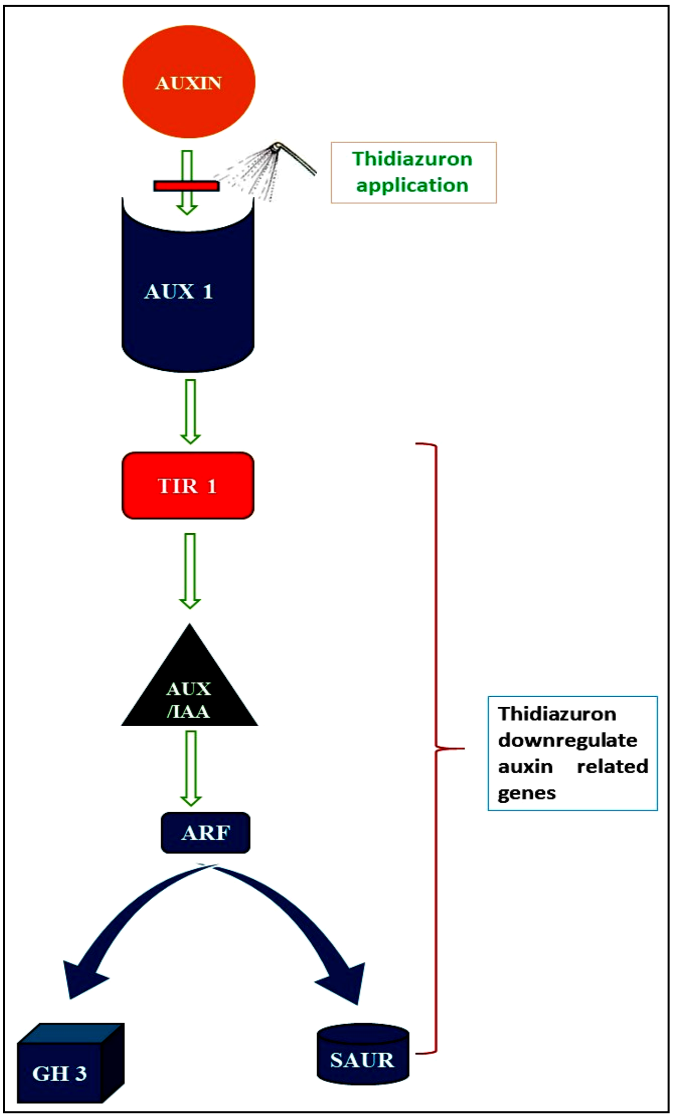

Fig. 2. Effect of foliar spray of thidiazuron on auxin signalling. Thidiazuron inhibits auxin transport by *AUX1* in the cell membrane, preventing the auxin from binding to the *TIR 1* receptor, an F-box protein functioning as an auxin receptor. This downregulation of *Aux/IAA* protein resulted in blocking ARF transcription factors involved in transcription of downstream corresponding auxin response genes and affecting GH3 and SAUR, decreasing leaf auxin content and promoting leaf abscission. ***AUX1*** : Auxin influx carrier proteins, ***TIR 1*** : Transport inhibitor response 1, ***Aux/IAA*** : Auxin/Indole-3-acetic acid family, ***ARF*** : Auxin response factors, ***GH3*** : Gretchen hagen 3, ***SAUR*** : Small auxin-up-regulated RNAs.

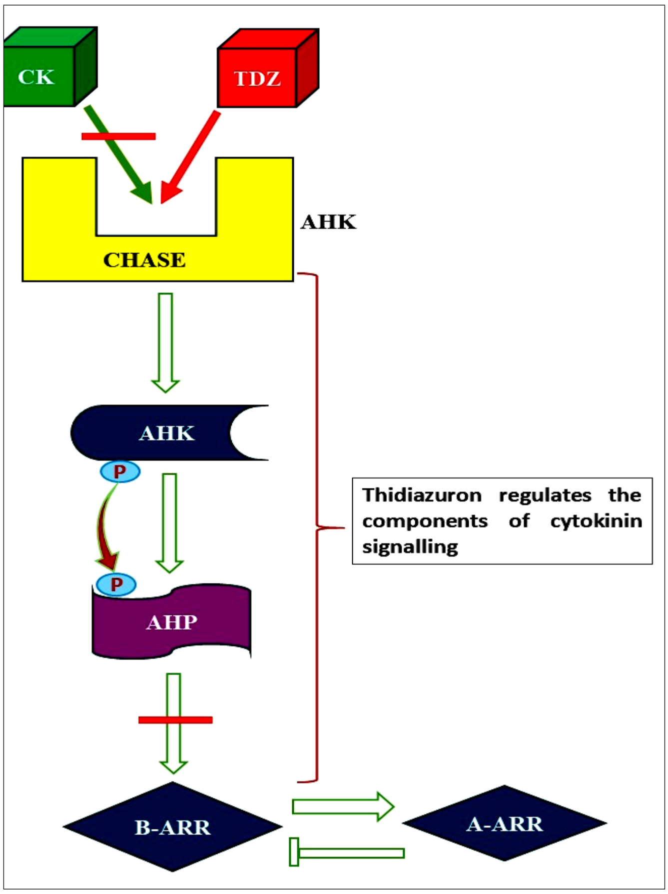

Fig. 3. Effect of foliar application of thidiazuron on cytokinin signalling. Thidiazuron (TDZ) inhibit the cytokinins signal transduction initiated through the perception of cytokinins by sensor *AHK*, preventing phosphorylation signalling cascade and phosphoryl group transfer from *AHK* to *AHP*. This inhibits the translocation of *AHP* from the cytoplasm to the nucleus, thereby inhibiting the activation of *ARR* transcription, reducing cytokinin production and promoting leaf abscission. **CK**: Cytokinin, ***AHK*** : *Arabidopsis* histidine kinase, ***AHP*** : *Arabidopsis thaliana* histidine phosphotransfer proteins, ***A-ARR*** : Type A - *Arabidopsis* response regulators, ***B-ARR*** : Type B - *Arabidopsis* response regulators.

Thidiazuron promotes gene expression of cytokinin synthesis and signaling in cotton

Cytokinin is another vital plant growth hormone that regulates various biological processes, including plant development, growth, and the delay of senescence (36, 37). It also significantly enhances stress tolerance by increasing soluble sugar content, acting as an osmoprotectant. Moreover, cytokinin is crucial in crop defoliation through its interaction with the ethylene signaling pathway and regulation of leaf abscission (Fig. 3). The application of chemical defoliants, such as thidiazuron and ethrel, significantly affects cytokinin levels in cotton, leading to plant defoliation (38).

Thidiazuron, in particular, downregulates genes involved in the cytokinin signaling pathway, including histidine kinase (*HK*) and histidine phosphotransferase (*HP*) proteins (36). Specifically, thidiazuron treatment in cotton plants downregulated the expression of 53 cytokinin signaling genes, which included 11 cytokinin histidine kinase receptor genes (*AHK*), one histidine-containing phosphotransferase gene (*AHP*), and 41 type-B cytokinin response regulators (*B-ARR*s). Cytokinin oxidase/dehydrogenase (*CKX*) is responsible for the oxidation and degradation of cytokinins, thereby controlling cytokinin homeostasis. The CKX gene is an important regulatory component in thidiazuron-induced leaf abscission by regulating cytokinin levels. Consequently, thidiazuron induces explicitly a decline in cytokinin content in cotton leaves (39). Furthermore, thidiazuron suppresses the expression of B-ARR (36).

Thidiazuron promotes gene expression of ethylene signaling in cotton

Ethylene is a multifunctional gaseous hormone commonly associated with defoliation. It plays a role in the defoliation process induced by various compounds, including auxins and cytokinins (35). Additionally, cotton leaf abscission in response to chemical defoliants is regulated by the interaction between the cytokinin and ethylene signaling pathways (40). Specifically, the application of thidiazuron mediates cotton defoliation by elevating endogenous ethylene production and disrupting the plant's balance of auxin and cytokinin hormones (20, 39). Numerous hormone-signalling genes are upregulated and downregulated in response to thidiazuron treatment. Thidiazuron application increases the expression of ethylene signaling genes, such as aconitase 3 (*ACO3*), acetyl-CoA synthetase (*ACS*), ethylene insensitive (*EIN*s), ethylene response factor 2 (ERF2), and ethylene receptor 1 (ETR1). Furthermore, cytokinin signaling genes, like cytokinin oxidase/ dehydrogenase (*CKX*), are upregulated, while the cytokinin response regulatory factors from Arabidopsis thaliana (*ARR*s) are downregulated. The downregulation of Transport Inhibitor Response 1 (*TIR*1) and Auxin Response Factor (*ARF*) affects auxin transport (12) (Fig. 4).

damage during application while requiring less water and a lower dilution ratio (46,47). Applying thidiazuron using conventional sprayers yields a defoliation rate comparable to that of UAVs (48). However, applying thidiazuron through UAVs enhances the defoliation rate, meeting the requirements for mechanical harvesting (49). When thidiazuron is sprayed on cotton using a multi-rotor UAV, a gradual increase in the defoliation rate is observed, with the most significant effects noted between five and fifteen days after treatment (50).

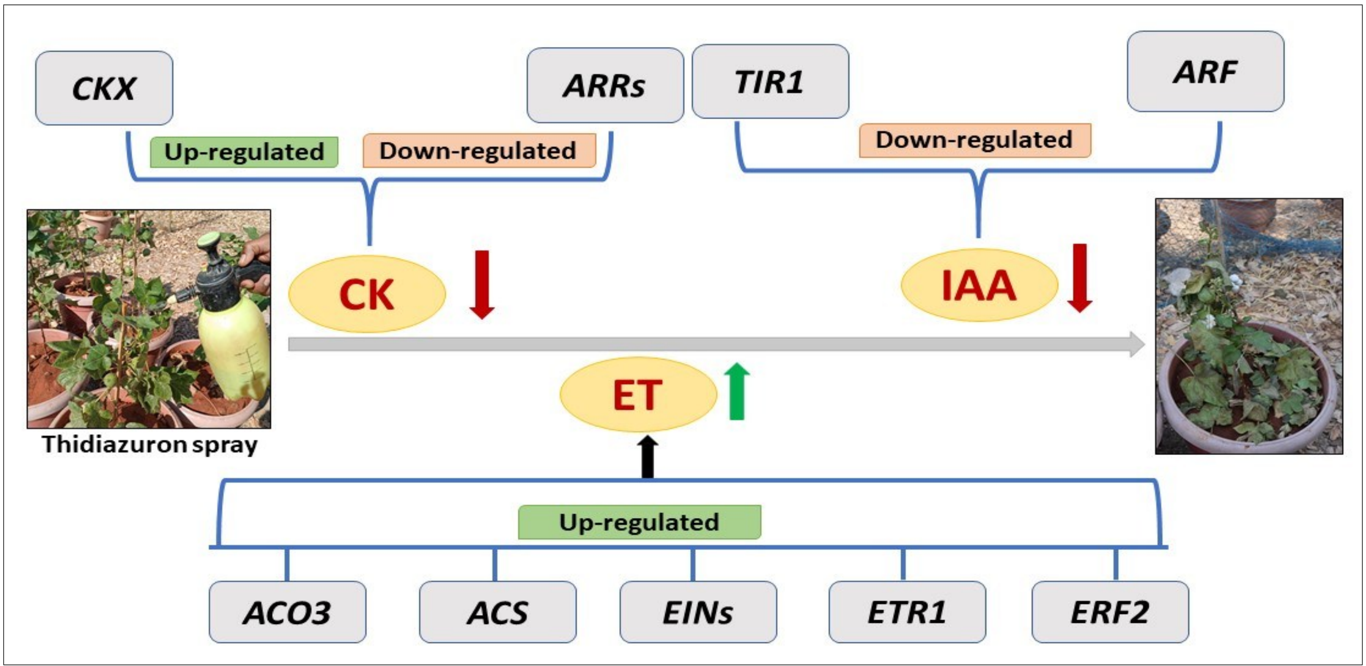

Fig. 4. Defoliant application influences phytohormonal gene expression. Thidiazuron induces ethylene production by upregulation of ethylene-related genes of aconitase 3 (***ACO3***), acetyl-CoA synthetase (***ACS***), ethylene insensitive (***EINs***), ethylene receptor1 (***ETR1***), ethylene response factor2 (***ERF2***) and cytokinin oxidation by upregulation cytokinin oxidase/dehydrogenase (***CKX***) in leaves. Additionally, thidiazuron downregulates cytokinin response regulatory factor, Arabidopsis (*Arabidopsis thaliana*) response regulators (***ARRs***), and Auxin related genes like transport inhibitor response 1 (***TIR 1***) and auxin response factors (***ARF***) results in lowering auxin and cytokinin production and promotes leaf abscission. Red down arrow and Green upward arrow indicate a decrease and increase in the production of phytohormones such as cytokinin (**CK**) and indole acetic acid (**IAA**) as well as ethylene (**ET**), respectively.

Method of thidiazuron application

The application of defoliants is crucial for the efficiency of cotton defoliation. Defoliants are typically applied during the 60-80% boll bursting stage. Enhancing the coverage of defoliants on cotton plants is crucial in improving their efficacy. However, many farmers still rely on human-operated machinery or ground equipment, such as conventional sprayers or tractor-mounted sprayers, which yield lower defoliation rates than aerial applications (14, 41). This inefficiency arises because the wheels of conventional ground-based sprayers can roll over cotton plants as they move through the fields, damaging branches and separating bolls. Such damage can lead to significant yield losses and excessive water usage to cover a given crop area (42).

Currently, researchers are utilizing unmanned aerial vehicles (UAVs) equipped with sprayers to apply defoliants to cotton, along with forecasting application amounts through remote sensing images (28). In UAVs, using ultra-low volume (ULV) sprayers has proven to be highly effective for defoliation in cotton (43, 44). The main advantages of ULV sprayers include reduced application rates, minimized drift, and less waste (45). ULV sprayers accurately deposit defoliants on the target crop area, avoiding physical

Conclusion

Thidiazuron is a potent defoliant that has become essential in modern cotton production. It significantly alters cotton plants' physiological and hormonal balance to induce abscission, which is necessary for efficient mechanical harvesting. Thidiazuron enhances leaf abscission and limits leaf regeneration, producing cleaner cotton with less contamination during harvesting. Thidiazuron also stimulates leaf drop by promoting ethylene production and inhibiting auxin transport, which are crucial for forming abscission zones. Whether aerial or ground spraying, application methods have proven effective in enhancing defoliation rates and yield during mechanization. Maximum effectiveness in cotton defoliation is achieved when thidiazuron is applied at 60 to 80% boll opening. In conclusion, thidiazuron is an effective defoliant contributing to sustainable cotton production, particularly when combined with mechanization.

Future Research Threats

In addition to the importance of thidiazuron in cotton defoliation, it is crucial to understand its mode of action in modulating plant hormones, including auxin, cytokinin, and ethylene, to ensure optimal application and high-quality cotton fiber production. Future challenges will involve advancing specific application methods to minimize environmental contamination and maximize coverage. Simultaneously, while technologies such as ultra-low volume spraying provide tremendous potential, factors such as flight duration, battery longevity, and mechanization expenses must also be considered. Additionally, there is a need for ongoing efforts toward sustainability, particularly concerning the environmental impact of defoliant use on non-target organisms and soil health. Moreover, achieving sustainable effects from thidiazuron on cotton defoliation requires careful management and continuous monitoring of associated risks to ensure its long-term effectiveness as a solution.

Authors' Contributions

RR and VR designed the paper's approach and structure and wrote the manuscript with input from all authors. AS[1], AS[2], KT, RJ, SS, and SA contributed to conceptualizing and provided academic input for the manuscript. All the authors reviewed, edited, and approved the final version of the manuscript. (AS[1]- Alagarswamy Senthil & AS[2]- Alagesan Subramanian)

Compliance with Ethical Standards

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

Ethical issues: None

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