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COMMENT

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Premature senescence in Bt Cotton: understanding the mechanisms and control measures

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Abstract

Premature senescence in *Bacillus thuringiensis* (Bt) cotton has emerged as a significant challenge to the formation and realization of fiber yield and quality since its commercialization in 1997. Initially, premature senescence was thought to be an inherent trait associated with the *Bt* gene. However, subsequent research and practice have demonstrated that it is not directly linked to the *Bt* gene but rather results from a physiological imbalance between the sink and source, as well as between the root and shoot in Bt cotton. This short review provides an overview of the causes, mechanisms, and control measures for premature senescence in Bt cotton. It offers valuable insights for future research and the sustainable application of transgenic crops.

Keywords Bt cotton, Premature senescence, Mechanisms, Control measures, Agronomic management

Bacillus thuringiensis (Bt) cotton has been widely cultivated in China since its introduction in 1997. By 2007, its planting area had reached 3.8 million hectares, accounting for 69% of the national cotton-planting area. By 2018, Bt cotton covered 95% of the total cotton area (Ho et al. 2009; Zhang et al. 2024). Despite its fast adoption, certain Bt cotton varieties have shown a propensity for premature senescence, leading to significant yield losses ranging from 10% to 30% (Zhang et al. 2024).

Premature senescence refers to the early termination of the plant's life cycle within the growing season (Chen et al. 2016). This phenomenon has intensified since the commercial release of Bt cotton in China. Initially, premature senescence was attributed to the *Bt* gene itself, but further research has revealed that it is primarily caused by physiological imbalances between the cotton plant's source (photosynthetic tissues) and sink (reproductive structures), as well as between its root and shoot systems (Chen et al. 2016; Zhang et al. 2024). This review traces the evolution of our understanding of the causes and mechanisms behind premature senescence in Bt cotton, highlighting effective prevention and control strategies, with an emphasis on agronomic management. It also provides insights for future research to address this critical issue.

The mechanism of premature senescence in Bt cotton

Premature senescence in Bt cotton is a multifaceted phenomenon influenced by genetic, physiological, and environmental factors. Initially, premature senescence was attributed to the *Bt* gene itself, with the hypothesis that the expression of Bt toxins might impair nutrient uptake and plant growth. Early studies suggested that Bt cotton is particularly sensitive to potassium deficiency, which could exacerbate senescence (Tian et al. 2008). However, subsequent research revealed that Bt cotton does not significantly differ from non-Bt cotton in terms of potassium utilization (Wang et al. 2022). Moreover,

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the expression of Bt toxin proteins has been shown to reduce pest damage to cotton flowers and bolls, reducing boll loss compared with non-Bt varieties. A number of studies have identified a crucial factor in premature senescence: the imbalance between the plant's source-sink relationship and root-shoot allocation (Li et al. 2012; Chen et al. 2016). Bt cotton tends to produce more bolls, which increases its demand for assimilates, yet the increased boll load reduces the allocation of photosynthetic products to the roots, impairing root development and leading to an inefficient source-sink relationship (Dong et al. 2008).

This imbalance ultimately induces early senescence. The root-shoot relationship is disrupted when the plant's aerial parts are heavily loaded with bolls, further limiting root growth and nutrient uptake (Chen et al. 2016). Experimental evidence supports the role of source-sink imbalance and root-shoot misallocation in triggering premature senescence. For example, the removal of early fruiting branches or grafting senescent-prone Bt cotton onto non-senescent rootstocks has been shown to delay premature senescence (Chen et al. 2018; Bilal et al. 2017). Conversely, stem girding, which disrupts the transport of assimilates, promotes leaf senescence (Dai et al. 2011). These findings underscore the importance of maintaining a balanced source-sink relationship and root-shoot allocation in preventing premature senescence in Bt cotton.

Contributing factors to premature senescence

Premature senescence in Bt cotton is influenced by genetic traits, environmental conditions, and cultivation practices (Table 1). Genetic factors also contribute to premature senescence, as some Bt cotton varieties are more prone to early senescence due to their specific genetic makeup and physiological responses. For example, certain genotypes may exhibit reduced root vigor or inefficient nutrient remobilization, making them more susceptible to senescence under stress conditions (Chen et al. 2016). Environmental stressors such as drought, high temperatures, and nutrient imbalances, particularly potassium deficiency, exacerbate senescence (Zhu et al. 2023; Wang et al. 2023; Ahmed et al. 2024; Nagaraj et al. 2024). These stressors disrupt physiological processes, leading to accelerated aging and reduced plant vigor. Endogenous plant hormones, including cytokinin, abscisic acid, auxin, gibberellin, ethylene, and jasmonic acid are associated with senescence, and considered to be involved in the regulation of senescence (Chen et al. 2016; Li et al. 2019a, b; Zhang et al. 2021). For instance, ethylene and abscisic acid are known to promote senescence, while cytokinins delay it. The application of plant growth regulators, such as mepiquat chloride, has been shown to delay vegetative growth, optimize plant architecture, and coordinate the relationship between vegetative and reproductive growth, thereby achieving normal maturity (Yeates et al. 2002; Al-Khayri et al. 2024). Cultivation practices, such as improper fertilization, low planting density, and inadequate crop management, can also influence the onset and severity of premature senescence (Chen et al. 2016; Li et al. 2019a, b; Zhang et al. 2021). For instance, excessive nitrogen application can lead to excessive vegetative growth at the expense of reproductive development, while insufficient potassium fertilization can exacerbate nutrient imbalances and accelerate senescence.

Table 1 Key causes of premature senescence in Bt cotton

Category	Contributing factors	Examples/details
Genetic factors	Specific genotypes with reduced root vigor, inefficient nutrient remobilization	Some Bt cotton varieties are inherently more prone to senescence under stress due to their genetic makeup (e.g., weak root systems)
Physiological disorders	Imbalances in source-sink relationships, root-shoot allocation issues	Increased boll load leads to poor nutrient allocation to roots, impairing development and causing senescence (Chen et al. 2016)
Environmental influences	Drought, high temperatures, waterlogging, salinity, and other abiotic stresses	Stress conditions disrupt physiological processes and accelerate aging (Zhu et al. 2023; Ahmed et al. 2024)
Nutrient deficiencies	Imbalances in nitrogen, potassium, phosphorus, and trace elements	Potassium deficiency is particularly critical, affecting photosynthesis and stress resistance (Wang et al. 2022; Tian et al. 2024)
Hormonal imbalance	Endogenous hormones affecting senescence (ethylene, cytokinin, auxin, gibberellin, etc.)	Ethylene and abscisic acid promote senescence, while cytokinin delays it (Chen et al. 2016; Zhang et al. 2021)
Agronomic practices	Improper fertilization, excessive nitrogen, low planting density, poor crop management	Excessive vegetative growth, nutrient imbalances, and suboptimal planting practices exacerbate senescence (Chen et al. 2016)

Genetic breeding strategies to address premature senescence

Targeted genetic breeding strategies, including heterosis utilization, gene editing, and the introduction of superior genetic traits, have proven effective in mitigating premature senescence.

Heterosis utilization

Crossbreeding Bt cotton with non-Bt varieties exhibiting improved source-sink relationships has proven effective in developing F_1 hybrids with enhanced anti-senescence traits and higher yields (Huang et al. 2024). These hybrid varieties, widely adopted in China around 2000, demonstrated superior performance in delaying senescence and improving productivity (Dong et al. 2004). However, high labor demands associated with hybrid seed production led to their gradual replacement by inbred cotton varieties with similar traits by 2010. Despite this shift, heterosis utilization remains a valuable strategy for enhancing the resilience and yield potential of Bt cotton.

Gene editing

By introducing superior genes from wild cotton species or related plants that exhibit resistance to premature senescence, new Bt cotton varieties with enhanced insect resistance and delayed senescence traits can be developed. Distant hybridization has been used to incorporate novel genetic resources that improve the cotton plant's overall stress resistance and adaptability (Chen et al. 2016; Ahmed et al. 2024). In recent years, advanced gene-editing technologies, such as CRISPR/Cas9, have shown significant potential for mitigating premature senescence in Bt cotton (Nagaraj et al. 2024). Modern gene-editing approaches focus on hormone metabolism genes, nutrient recycling genes, and transcription factors (TFs) associated with cotton leaf senescence. For instance, Liu et al. (2012) transferred *IPT* gene into the premature senescence-prone upland cotton variety (CCRI 10) using the pollen tube channel technique, resulting in delayed senescence, improved lint yield, and enhanced fiber quality. Editing genes involved in ethylene synthesis or signaling, which play a pivotal role in the senescence process, can effectively delay the senescence of cotton leaves and plants (Zhang et al. 2023). Expression of Arabidopsis *AtNLP7* gene in cotton improved nitrogen use efficiency and yield under both low and high nitrogen conditions (Jan et al. 2022). Similarly, overexpression of the *AGL42* gene in cotton delayed leaf senescence through the down-regulation of NAC transcription factors (Latif et al. 2022). Among transcription factors, NAC and WRKY are the most extensively studied regulators of leaf senescence (Cao et al. 2023). Ectopic expression of *GhNAP* in cotton rescued the null atnap phenotype in *Arabidopsis*, and the GhNAPi lines of cotton displayed delayed leaf senescence without compromising other agronomic traits (Bengoa Luoni et al. 2019). This approach offers a precise and efficient means of improving the anti-senescence capabilities of Bt cotton, offering valuable biological breeding resources (Chen et al. 2015; Bengoa Luoni et al. 2019).

Agronomic practices to mitigate premature senescence

Effective agronomic practices include: rational fertilization, plant topping and removal of early fruiting branches, late sowing and high plant density, and soil tillage and straw returning.

Rational fertilization

Proper fertilization, particularly the balanced application of nitrogen, phosphorus, potassium, and trace elements, is essential for promoting healthy plant growth and preventing premature senescence (Yang et al. 2017; Song et al. 2020). Sufficient organic fertilizer can improve soil fertility, enhance nutrient retention, and boost root development, all of which contribute to delayed senescence (Kong et al. 2011; Chen et al. 2016; Shao et al. 2023). Maintaining appropriate levels of potassium and nitrogen in the soil is especially critical for preventing early senescence (Dong et al. 2010; Tian et al. 2024).

Plant topping and removal of early fruiting branches

Timely topping and the removal of early fruiting branches can help regulate plant growth, optimize source-sink relationships, and delay senescence. Studies have shown that removing the lower fruiting branches can help improve the plant's nutrient distribution and prevent premature senescence (Chen et al. 2018; Zhai et al. 2018). However, it is important to balance the removal of vegetative branches, as retaining certain branches may enhance senescence resistance (Dong et al. 2008).

Late sowing and high plant density

Adjusting the sowing date and increasing plant density can synchronize the cotton plant's growth stages and enhance photosynthetic efficiency (Dai et al. 2015; Manibharathi et al. 2024). For example, delayed sowing combined with high plant density reduces the incidence of premature senescence by optimizing boll formation and maturity (Li et al. 2019a, b; Chen et al. 2022; Lakshmanan et al. 2025).

Soil tillage and straw returning

Deep tillage and straw returning to the soil improve soil structure, enhance water retention, and promote root development, all of which contribute to better stress tolerance and delayed senescence (Qi et al. 2022). These practices increase organic matter content and improve the soil's water-holding capacity and nutrient retention, creating a favorable environment for root development (Luo et al. 2018; Li et al. 2019a, b).

In summary, premature senescence in Bt cotton is a complex issue influenced by genetic, physiological, and environmental factors. While early research mistakenly attributed senescence to the *Bt* gene, it is now understood that imbalances in source-sink relationships and root-shoot dynamics are the primary causes. Agronomic practices such as rational fertilization, plant topping, late sowing, high plant density, and soil management offer effective solutions to mitigate premature senescence. These practices, combined with genetic breeding, provide a comprehensive approach to improving the resilience and productivity of Bt cotton. This review offers insights into the complex nature of premature senescence and highlights the integrated approaches required for its control, contributing to the sustainable development of Bt cotton and other genetically modified crops worldwide.

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Chen YZ and Dong HZ wrote the comment.

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Data availability
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Declarations

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Not applicable.

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