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Molecular physiology of abiotic stress in cotton reproduction: Current knowledge and future perspectives

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Abstract

This review article comprehensively examines the impact of abiotic stresses on cotton reproductive physiology and boll development. It highlights how drought, heat, salinity, and nutrient deficiency disrupt cotton's reproductive processes, leading to reduced boll retention, malformed bolls, and diminished fiber quality. The article delves into the cellular mechanisms, elucidating how these stressors trigger membrane destabilization, reactive oxygen species accumulation, and hormonal imbalances that impair photosynthesis and carbohydrate allocation to developing bolls. Drought stress is emphasized for its severe effects, including reduced tissue water potential and impaired cell expansion during boll development. It also upregulates ABA biosynthesis, leading to stomatal closure and accelerated floral abscission. Heat stress is shown to compromise pollen viability and stigma receptivity, exacerbating boll abortion through ethylene-mediated abscission. Salinity stress induces ionic toxicity and disrupts auxin and gibberellin signalling, vital for ovule development. Nutrient deficiencies, particularly boron and potassium, further impair pollen tube growth and osmotic regulation. The article underscores the critical role of hormonal regulation in reproductive resilience, noting how elevated ABA and ethylene levels antagonize gibberellins and cytokinin's. It also discusses targeted interventions, such as ethylene inhibitors like 1-MCP, which can mitigate stress-induced boll drop. Furthermore, the review explores advancements in breeding stress-tolerant cotton cultivars by leveraging physiological and molecular traits, and the use of molecular tools to identify resilience-associated genes. The review emphasizes the need for a multidisciplinary approach integrating traditional breeding, molecular genetics, and precision agronomy to safeguard cotton's reproductive potential amid climate variability. By understanding the intricate interplay between stress responses and reproductive physiology, researchers can pave the way for sustainable cotton production in an increasingly unpredictable environment.

Keywords: Cotton (*Gossypium* spp.), abiotic stress, reproductive physiology, boll development, hormonal regulation

Introduction

Cotton (Gossypium spp.) represents a globally significant agricultural commodity, serving as the principal source of natural fiber for textile manufacturing while making substantial contributions to the vegetable oil market. As a crop predominantly cultivated in tropical and subtropical regions - with major production centers in India, China, Pakistan, the United States, and Brazil - cotton faces mounting challenges from various abiotic stressors including drought, elevated temperatures, soil salinity, and nutrient deficiencies (Iqbal *et al*., 2023; Rehman *et al*., 2024) [16, 28]. These environmental constraints significantly impair both vegetative growth and reproductive development, manifesting as reduced boll retention, abnormal boll formation, and compromised fiber characteristics (Singh *et al*., 2023) [36]. At the molecular level, abiotic stresses induce cellular perturbations including membrane instability, accumulation of reactive oxygen species (ROS), and disruption of hormonal equilibrium, collectively resulting in impaired photosynthetic efficiency and disrupted carbohydrate partitioning to developing reproductive structures (Zhi *et al*., 2024; Dalvi *et al*., 2023) [50, 5]. The reproductive phase - encompassing floral initiation, anthesis, and boll maturation - demonstrates particular vulnerability to environmental stresses due to its dependence on precise hormonal coordination and maintenance of optimal source-sink relationships (Rehman *et al*., 2024) [28]. In the context of escalating climate variability, elucidating the physiological and molecular basis of stress adaptation has emerged as a critical research priority for ensuring sustainable cotton production. Drought stress emerges as the most detrimental abiotic factor, causing reduction in tissue water potential and inhibition of cell expansion during critical boll development stages (Iqbal *et al*., 2023) [16]. Water deficit conditions stimulate abscisic acid (ABA) biosynthesis, leading to stomatal closure and consequent limitation of photosynthetic capacity, while simultaneously promoting premature floral abscission (Azhar *et al*., 2023) [1]. Thermal stress exceeding 35°C similarly disrupts reproductive success by impairing pollen viability and stigma functionality, with subsequent boll abortion mediated through ethylene-regulated abscission pathways (Ekinci *et al*., 2023; Chen *et al*., 2024) [9, 4]. Salinity stress compounds these challenges through ionic toxicity (Na^+ and Cl^- accumulation) and interference with auxin and gibberellin signaling cascades essential for proper ovule development (Zhi *et al*., 2024) [50]. Micronutrient deficiencies, particularly boron and potassium, further exacerbate reproductive impairments by disrupting pollen tube elongation and osmotic homeostasis (Dalvi *et al*., 2023) [5]. These environmental stressors collectively perturb hormonal balance, characterized by elevated ABA and ethylene levels that antagonize the activity of gibberellins and cytokinins - phytohormones critical for floral and boll development (Chen *et al*., 2024) [4]. Emerging mitigation strategies, including application of ethylene inhibitors such as 1-methylcyclopropene (1-MCP), demonstrate potential for ameliorating stress-induced boll abscission, underscoring the pivotal role of hormonal regulation in reproductive resilience (Chen *et al*., 2024) [4]. Contemporary breeding initiatives are increasingly incorporating physiological and molecular markers to develop stress-adapted cultivars. Key selection criteria include pollen viability indices, boll retention capacity, and membrane thermostability (Singh *et al*., 2023) [37]. The integration of advanced molecular tools - including quantitative trait loci (QTL) mapping, marker-assisted selection, and CRISPR-based genome editing - has accelerated identification of stress-responsive genes such as GhCCL, which confers enhanced boll development under adverse conditions (Dhandapani *et al*., 2024) [7]. A holistic approach combining conventional breeding methodologies with molecular genetics and precision agriculture technologies will be essential for preserving cotton's reproductive capacity in the face of climate uncertainty. Through comprehensive understanding of the complex interactions between stress response mechanisms and reproductive physiology, the scientific community can develop innovative solutions to maintain sustainable cotton production systems under increasingly variable environmental conditions.

Overview of Cotton Reproductive Physiology

Cotton (*Gossypium* spp.) exhibits a sophisticated reproductive program governed by intricate physiological, hormonal, and environmental regulatory networks. A comprehensive understanding of floral ontogeny, pollination mechanisms, fertilization processes, and boll maturation is paramount for identifying stress-sensitive developmental windows. This section systematically examines cotton's reproductive chronology and the source-sink relationships fundamental to boll formation and yield optimization (Zhang *et al*., 2023) [48].

1. Floral Bud Development and Anthesis

The reproductive cycle commences with floral bud initiation at axillary meristems of sympodial branches, typically occurring 35-40 days post-sowing under optimal conditions (Oosterhuis, 2021) [23]. Environmental cues including temperature regimes and photoperiod, coupled with endogenous hormonal signals, precisely regulate this developmental transition. The floral bud (commonly termed "square") undergoes sequential morphological transformations over a 21-24-day period before anthesis. Flower opening, predominantly occurring at dawn and lasting approximately 24 hours, represents the phenological stage where complete stamen (male) and carpel (female) functionality is achieved (Chen & Wang, 2022) [2]. While cotton predominantly exhibits self-pollination, entomophilous cross-pollination occurs with measurable frequency under field conditions (Pervez *et al*., 2021). Pollen deposition on stigmatic surfaces during anthesis initiates the fertilization cascade.

2. Pollination and Fertilization

The pollination process demonstrates strict temporal synchronization with anthesis, requiring efficient transfer of viable pollen grains to receptive stigmatic surfaces (Singh & Reddy, 2023) [37]. Subsequent pollen tube elongation represents an energetically demanding process, navigating through stylar tissues via chemotropic guidance mechanisms. Double fertilization is achieved through sperm cell release, with one gamete fusing with the egg cell (zygote formation) while the other combines with central cell nuclei (endosperm development) (Li *et al*., 2022). This critical reproductive phase exhibits particular vulnerability to environmental stressors, with successful fertilization constrained to a narrow 24-48 hour post-anthesis window. Both pollen viability and stigma receptivity demonstrate pronounced thermosensitivity, where supraoptimal temperatures (>35°C) induce stigmatic desiccation and pollen enzyme denaturation, ultimately compromising fertilization success (Kumar *et al*., 2021).

3. Embryo and Boll Development

Post-fertilization developmental progression encompasses embryogenesis and boll formation, with the fertilized ovule differentiating into the seed and surrounding tissues constituting the protective fruiting structure (Tang *et al*., 2023). Boll maturation follows a triphasic developmental trajectory: (1) cellular proliferation (0-15 DPA), (2) cellular elongation (15-30 DPA), and (3) secondary cell wall deposition (30-45 DPA) (Oosterhuis & Jernstedt, 2020) [24]. Each developmental phase necessitates distinct metabolic and structural modifications. The elongation phase facilitates remarkable fiber cell extension (up to 3 cm), mediated by turgor-driven expansion and coordinated activity of cell wall modifying proteins including expansins, aquaporins, and cellulose synthase complexes (Haigler *et al*., 2022) [12]. Optimal water relations and hormonal homeostasis, particularly auxin and gibberellin balance, constitute critical determinants of these developmental processes.

4. Boll Maturation and Dehiscence

The maturation phase witness's substantial carbohydrate mobilization into developing bolls to support cellulose biosynthesis (Zhao *et al*., 2023) [49]. Final boll dehiscence, exposing mature lint for harvest, is regulated by dynamic hormonal shifts - specifically declining auxin concentrations coupled with ethylene biosynthesis upregulation, which collectively facilitate carpel wall separation (Chen *et al*., 2021) [3]. Both boll retention capacity and ultimate size serve as primary yield determinants, with even minor developmental perturbations (from abiotic stress, hormonal imbalance, or biotic factors) potentially inducing premature abscission or defective fiber development (Iqbal *et al*., 2022) [40].

5. Source-Sink Dynamics in Reproductive Growth

Cotton's reproductive success hinges on efficient source-sink coordination, balancing photoassimilate production (primarily mature leaves) with reproductive sink demand (developing bolls) (Wang *et al*., 2023). The reproductive phase triggers metabolic prioritization toward sink organs, with sucrose and related photoassimilates being phloem-mobilized to developing bolls during peak filling stages. Abiotic stressors including drought and nutrient limitations disrupt this equilibrium through photosynthetic inhibition and phloem transport impairment, creating "sink limitation" scenarios that manifest as reduced boll dimensions, compromised fiber maturity indices, and diminished seed weights (Azhar *et al*., 2022) [1]. Hormonal regulation of carbohydrate partitioning is evident, where cytokinins stimulate mitotic activity during early boll development, while gibberellins and auxins govern subsequent elongation and expansion phases (Singh *et al*., 2021). Stress-induced

ABA accumulation negatively impacts sink strength by accelerating leaf senescence and inducing stomatal closure, thereby constraining photosynthetic carbon assimilation (Haigler *et al*., 2022) [12].

6. Hormonal Regulation of Reproductive Development

Phytohormones constitute the master regulatory network coordinating cotton reproductive development:

- **Auxins:** Govern floral initiation, ovule differentiation, and early boll formation while maintaining sink competitiveness and modulating ethylene sensitivity (Oosterhuis, 2021) [23]
- **Cytokinins:** Direct cell cycle progression and ovule establishment, with stress-mediated cytokinin reduction correlating with impaired boll set (Zhang *et al*., 2023) [48]
- **Gibberellins:** Mediate cellular elongation and fiber extension processes, exhibiting particular sensitivity to hydrostatus (Chen & Wang, 2022) [2].
- **Abscisic Acid (ABA):** Functions as the central stress-response regulator, with elevated concentrations under drought and salinity promoting abscission through growth hormone antagonism (Kumar *et al*., 2021)
- **Ethylene:** Accelerates floral and boll abscission under heat and drought stress conditions (Chen *et al*., 2021) [3].

Therapeutic applications of hormonal modulators, particularly ethylene perception inhibitors like 1-methylcyclopropene (1-MCP), have demonstrated efficacy in mitigating stress-induced boll abscission and preserving lint yields (Tang *et al*., 2023).

7. Structural and Molecular Determinants of Reproductive Stress Sensitivity

Cotton reproductive structures exhibit inherent stress susceptibility due to specific anatomical features: vacuolate fiber cells, delicate stigmatic surfaces, and specialized vascular connections (Zhao *et al*., 2023) [49]. Molecular investigations have identified stress-responsive genetic elements (e.g., *GhDREB*, *GhHSP*, *GhCCL*) that are differentially expressed in reproductive tissues under abiotic stress, revealing endogenous protective mechanisms (Dhandapani *et al*., 2022) [6]. Nevertheless, reproductive organs consistently demonstrate reduced stress resilience compared to vegetative tissues, attributable to: (1) tissue-specific gene expression patterns, (2) limited cuticular development, and (3) the substantial metabolic investment required for gametogenesis and fertilization processes (Wang *et al*., 2023).

Drought Stress and Reproductive Failure in Cotton

Drought stress is a significant abiotic constraint in global cotton cultivation, severely impacting reproductive development and yield. The following section discusses the physiological, biochemical, and hormonal disruptions caused by drought stress, highlighting their convergence in inducing reproductive failure.

1. Impact on Floral Bud Initiation

Floral bud initiation in cotton requires sustained water availability, photosynthate production, and hormonal coordination. Drought conditions reduce soil moisture, leading to decreased turgor pressure and impaired cell expansion in the shoot apical meristem. This inhibits the transition from vegetative to reproductive growth, resulting in fewer floral buds, delayed flowering, and reduced fruiting sites (Saleem *et al*., 2015) [31]. Additionally, drought affects cytokinin transport from roots to shoots, a hormone that promotes meristematic activity and floral initiation. The decline in cytokinin levels under drought conditions impairs cell division in apical tissues, stunting floral development (Padmalatha *et al*., 2012) [25].

2. Pollen Viability and Fertilization Disruption

Pollen development and viability are highly sensitive to drought. Even short-term drought episodes during the squaring and flowering stages significantly reduce pollen viability, anther dehiscence, and stigma receptivity (Hu *et al*., 2020) [15]. Lower activity of enzymes such as ADP-glucose pyrophosphorylase and α-amylase under drought conditions impairs starch biosynthesis and breakdown, starving the growing pollen tube of essential ATP and carbon skeletons (Hu *et al*., 2019) [15]. This slows pollen tube elongation, reducing the probability of successful ovule fertilization. Drought-induced oxidative stress leads to membrane lipid peroxidation in pollen grains, further reducing their viability (Zare *et al*., 2014).

3. Ovule Fertilization and Post-Zygotic Development

Reduced water potential in ovule tissues under stress leads to the collapse of nucellar cells and poor receptivity of the synergid cells, which guide the pollen tube. This impedes successful double fertilization and embryo formation (Hu *et al*., 2020) [15]. The embryo sac requires a constant flow of carbohydrates and water, which is hampered during drought due to impaired phloem loading. In stressed pistils, a significant decline in stored starch and sucrose hydrolysis enzymes results in lowered glucose/fructose levels and ATP production (Hu *et al*., 2019) [14]. These factors severely limit seed and boll set, and any fertilized ovules that survive are often too weak to mature into full-sized seeds.

4. Stomatal Closure, Photosynthesis, and Carbohydrate Limitation

Under drought conditions, cotton plants rapidly accumulate ABA, triggering stomatal closure to conserve water. However, this simultaneously reduces CO_2 uptake and photosynthetic activity (Rahman *et al*., 2008) [29]. As a sink-sensitive crop, cotton depends heavily on leaf-produced sugars for reproductive development. Drought-induced carbohydrate shortages lead to either floral abortion or premature boll drop (Pilon, 2014). Additionally, water stress impairs phloem loading, restricting sugar transport to developing ovaries and fibers. This energy deficit disrupts critical cellular processes like mitosis and cell expansion (Padmalatha *et al*., 2012) [25].

5. ABA and Ethylene-Mediated Floral Abscission

Under drought, ABA levels in cotton tissues rise significantly, leading to early stomatal closure and the onset of senescence in source leaves (Iqbal *et al*., 2017) [40]. ABA also induces ethylene biosynthesis by upregulating 1-aminocyclopropane-1-carboxylic acid synthase (ACS) genes. Ethylene, in turn, triggers abscission zone (AZ) activation at the peduncle base, promoting cell separation and floral shedding (Chen *et al*., 2014) [4]. Ethylene-sensitive genotypes display higher square and boll shedding under drought. Conversely, treatments with 1-MCP, an ethylene receptor blocker, have been shown to reduce abscission and improve boll retention under stress (Chen *et al*., 2014 [3].

Reproductive Trait	Observed Impact Under Drought	Primary Cause	Supporting Studies
Floral bud initiation	Reduced number and delayed formation	Inhibited cytokinin transport; downregulation of FT genes	Saleem *et al*., 2015; Padmalatha *et al*., 2012 [31, 25]
Pollen viability	↓ 30–60% in drought-sensitive genotypes	Disrupted carbohydrate metabolism, oxidative stress	Hu *et al*., 2019; Zare *et al*., 2014 [14]
Ovule fertilization	Reduced fertilization success	Sucrose accumulation; low ATP in pistils	Hu *et al*., 2019; Hu *et al*., 2020 [14, 15]
Boll set and retention	Boll shedding increased by 40–70%	Ethylene production; carbohydrate shortage	Pilon, 2014; Chen *et al*., 2014 [3]
Photosynthetic rate	Declines 30–50% within 7–10 days of stress onset	ABA-induced stomatal closure	Rahman *et al*., 2008 [29]
Sugar translocation to bolls	Reduced by 50% in stressed plants	Impaired phloem loading, lower sucrose synthase activity	Padmalatha *et al*., 2012 [25]
Embryo development	Arrested or malformed embryos	Lack of metabolic substrates in ovule tissues	Hu *et al*., 2020 [15]

Heat Stress and Boll Development Disruption in Cotton

1. Critical Temperature Thresholds Affecting Flowering and Boll Retention

Cotton exhibits optimal reproductive development within a diurnal temperature range of 28–32 °C. Exposure to temperatures beyond this range, especially sustained highs above 35 °C during squaring and flowering, leads to irreversible damage to reproductive tissues (Song *et al*., 2014). For example, in controlled growth chambers, boll production was reduced by 65% when cotton flowers were exposed to 40 °C for five days during the tetrad stage of pollen development (Masoomi-Aladizgeh *et al*., 2020) [21]. Similar reductions were reported by Song *et al*. (2015), who found that square lengths <6 mm—corresponding to the sporogenous to tetrad stage—are particularly heat-sensitive. Boll retention was found to be positively correlated with pollen germination rates and negatively correlated with temperatures during floral organogenesis (Song *et al*., 2014). Recent studies have also shown that high temperatures can significantly reduce pollen viability and boll retention, highlighting the critical nature of temperature thresholds in cotton reproduction (Wang *et al*., 2021).

2. Heat-Induced Pollen Deformation and Fertilization Impairment

Pollen development is the most temperature-sensitive process in plant reproduction. In cotton, pollen undergoes meiosis and mitosis within the protective microsporangia; however, heat disrupts microtubule polymerization and protein folding essential to gametogenesis. Exposure to 40 °C significantly reduced pollen size and viability, especially at the tetrad and uninucleate stages (Masoomi-Aladizgeh *et al*., 2020) [21]. Proteomic analyses revealed that heat-stressed pollen exhibited reduced abundance of cytoskeletal and metabolic proteins, with a concurrent upregulation of heat shock proteins (HSPs), splicing factors, and chaperones (Masoomi-Aladizgeh *et al*., 2021) [22]. Despite these adaptive responses, impaired protein trafficking and endomembrane dysfunction—especially involving Rab proteins—were identified as limiting factors for pollen function under extreme heat. Additionally, *in vitro* studies indicate a sharp drop in pollen germination beyond 35 °C.

3. Stigma Desiccation and Female Reproductive Sensitivity

While male sterility under heat stress is well-documented, recent studies have emphasized the equally critical role of pistil vulnerability. Wang *et al*. (2021) demonstrated that heat-exposed pistils exhibit reduced water content, poor pollen adhesion, and disrupted pollen tube guidance due to ROS accumulation and cell wall disintegration in the transmitting tissue. This desiccation of stigmatic surfaces, coupled with reduced extracellular matrix proteins, compromises fertilization success even when viable pollen is available. The decline in successful pollen-pistil interactions contributes to the failure of seed set and initiates premature floral abscission.

4. Heat Shock Proteins and Thermoprotective Mechanisms

Heat shock proteins (HSPs) are molecular chaperones that mitigate protein misfolding under stress. In cotton, pollen proteomics revealed elevated levels of Hsp70 and Hsp90 families after heat exposure, indicating a heat acclimation response (Masoomi-Aladizgeh *et al*., 2020) [21]. These proteins assist in maintaining the structural integrity of cytoskeletal proteins, ensuring vesicle trafficking and cellular homeostasis during heat episodes. Transgenic and mutant studies suggest that enhancing HSP expression can extend pollen viability under heat stress. The challenge, however, lies in the temporal specificity—HSP induction must coincide with critical reproductive stages to be effective.

5. Antioxidant Enzymes and Reactive Oxygen Species (ROS) Management

Heat stress induces oxidative stress through excessive ROS accumulation in reproductive tissues. ROS are detrimental to DNA, membranes, and enzymatic machinery, causing cell death in gametophytic and sporophytic tissues. Rehman *et al*. (2021) [28] reported that heat-tolerant genotypes showed higher activity of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD). These enzymatic defenses delay cellular damage, enhance pollen viability, and improve boll retention under heat episodes. Moreover, Singh *et al* [37]. (2018) used antioxidant activity as a selection criterion in breeding programs, successfully identifying heat-resilient genotypes.

Salinity Stress: Ionic Imbalance and Reproductive Decline in Cotton

1. Na^+ and Cl^- Accumulation in Reproductive Tissues

Salt stress leads to excessive uptake of Na^+ and Cl^- ions, which accumulate in leaves and reproductive organs, displacing essential nutrients like potassium (K^+) and calcium (Ca^{2+}). The disruption in ion homeostasis impairs cellular metabolism in developing bolls and ovules. Studies on Indian upland cotton varieties under induced saline conditions (EC = 3.10 dS/m) demonstrated a significant reduction in boll weight, lint yield, and seed index, with increased Na^+ and decreased K^+/Na^+ ratios in ovular tissues (Dinakaran *et al.*, 2012) [8]. The high Na^+ concentration compromises membrane stability and enzyme activity, especially in reproductive cells, resulting in premature cell death and poor seed set (Sharma & Brar, 2005) [34]. Ion toxicity not only disturbs membrane integrity but also causes reduced water potential in developing bolls, stalling assimilate transport. Zafar *et al.* (2021) [46] found that high Na^+ accumulation decreased seed mass per boll and increased the proportion of undeveloped seeds in sensitive genotypes, while tolerant crosses (e.g., IUB-65 × FH-312) maintained higher K^+/Na^+ ratios and better boll retention. Recent studies have also shown that salt tolerance in cotton is associated with controlling Na^+ and Cl^- transport across roots and maintaining high K^+ levels in root and leaf mesophyll cells (Iqbal *et al.*, 2024) [17].

2. Disruption of Hormonal Balance

Salinity stress affects the levels and distribution of key phytohormones involved in reproductive development—namely, auxins (IAA), gibberellins (GA), and abscisic acid (ABA). A significant decline in auxin and GA activity in ovules and boll walls has been reported under saline irrigation conditions (Sharif *et al.*, 2019) [33]. Auxins are essential for ovule development and seed set. Under salinity, reduced IAA synthesis in reproductive tissues results in decreased sink strength, making ovules less competitive for assimilates (Sharma & Brar, 2005) [34]. This hormonal deficiency promotes boll shedding and increases the percentage of parthenocarpic (seedless) bolls. Similarly, GA deficiency leads to impaired fiber elongation and secondary wall deposition. Experimental work by Venkateshwarlu & Vardhini (2021) in the saline soils of Nizamabad, India, showed that application of exogenous salicylic acid (SA) mitigated salinity-induced hormonal imbalance and improved flower retention and boll development. Furthermore, the elevated levels of ABA under salinity conditions act antagonistically to auxins and gibberellins, promoting floral abscission and early senescence of reproductive structures (Sharif *et al.*, 2019).

3. Physiological and Biochemical Disruptions in Boll Development

Salinity stress severely reduces net photosynthesis and chlorophyll content while inhibiting carbohydrate metabolism, ultimately diminishing the plant's source strength (Sharma & Brar, 2005) [34]. The accumulation of osmolytes like soluble sugars in vegetative tissues under salt stress diverts assimilates away from developing bolls, increasing source-sink imbalance and increasing boll abortion rates. Additionally, salinity induces oxidative stress through excessive ROS production, damaging cellular membranes and enzymes in reproductive tissues. However, salt-tolerant cultivars such as CCRI-44 exhibit enhanced activity of antioxidant enzymes (SOD, CAT, POD), which helps mitigate oxidative damage and maintain better boll weight and reproductive success under saline conditions (Zhang *et al.*, 2012) [47]. These physiological adaptations highlight the critical role of antioxidant defense systems in preserving cotton productivity under salt stress. Recent investigations have also shown that salinity stress can lead to high Na^+ and Cl^- accumulation in leaves, adversely affecting photosynthesis, vegetative growth, and seed yield (Wahid *et al.*, 2004) [41].

Table 2: Boll Development Parameters Under Different Salinity Levels (Indian and Global Studies)

Salinity (EC, dS/m)	Genotype / Study	Avg. Boll Weight (g)	Boll Retention (%)	Seed Index (g)	Key Reference
0 (Control)	JK-4, PH 1009	4.0	92	9.8	Yadav (2015) [44]
3.10	32 Indian upland varieties	3.5	85	8.7	Dinakaran *et al.* (2012) [8]
4.0	LH 1556	3.2	78	8.1	Sharma & Brar (2005) [34]
6.0	Bikeneri Nerma	2.8	72	7.5	Bhute *et al.* (2012)
8.0	PH 1009 (stress-tolerant)	2.6	68	7.2	Yadav (2015) [44]
9.0	Upland cotton meta-analysis	2.2	60	6.4	Paknejad *et al.* (2020)
10.5–11.0	CCRI-79 (tolerant) + K applied	3.0	70	7.8	Ju *et al.* (2021)

Nutrient Deficiency and Boll Abortion in Cotton

1. Role of Nitrogen in Reproductive Growth and Boll Retention

Nitrogen is a fundamental macronutrient for cellular metabolism, chlorophyll synthesis, and reproductive organ development. Adequate nitrogen availability enhances the formation of sympodial branches, flower production, and seed set. Conversely, nitrogen deficiency during flowering reduces leaf area index (LAI), chlorophyll content, and photosynthetic capacity, leading to carbohydrate limitation in developing bolls (Gerik *et al.*, 1994) [11]. Studies have shown that low N levels reduce the number of bolls per plant, boll size, and boll weight. Yuan *et al.* (2018) [45] reported that under N-deficient conditions, boll weight and boll shell protein content were significantly reduced, coinciding with increased protease and peptidase activity—indicative of protein degradation. Boll shell nitrogen was prioritized to developing seeds, resulting in weaker structural development. Additionally, low N levels suppress enzymatic activity critical for amino acid metabolism in subtending leaves and reproductive tissues.

2. Potassium Deficiency and Reproductive Impairment

Potassium (K) is indispensable for phloem loading, osmotic regulation, and translocation of carbohydrates to bolls. Its role becomes critical during flowering and peak boll development, where deficiencies impair sugar transport, turgor maintenance, and enzymatic activity (Pettigrew & Meredith, 1997) [26]. Hu *et al.* (2016) [13] demonstrated that K-deficient cotton cultivars exhibited lower nitrate reductase and glutamate-pyruvate transaminase activity in the leaves subtending bolls, correlating with poor nitrogen assimilation and reduced boll biomass. In addition, free amino acid content increased in K-deficient treatments, indicating enhanced protein breakdown and reduced biosynthetic activity in developing boll tissues. In Indian conditions, showed that application of 150 kg K_2O ha^{-1}

significantly increased boll number and weight across varieties. However, without adequate potassium, symptoms of boll abortion, shortened fiber length, and reduced micronaire values were prominent. Late-season potassium deficiency is particularly detrimental, coinciding with high demand during boll expansion. Pettigrew *et al*. (1996) [27] reported that insufficient K supply during boll maturation reduced lint percentage and seed index by 9% and 4%, respectively.

3. Boron Deficiency and Pollen-Pistil Dysfunction

Boron (B) is essential for pollen tube elongation, cell wall structure, and membrane integrity. Deficiency leads to reproductive anomalies, including sterility, floral abscission, and boll abortion. Moreover, boron deficiency decreases IAA levels, disrupting hormonal gradients essential for ovule fertilization and seed set. In cotton, pollen grains produced under B-deficiency exhibit impaired germination and tube growth. Shu (1999) [35] demonstrated that insufficient B reduced protein content in bolls and fiber elongation, resulting in weak boll retention. Boron also interacts with nitrogen: its availability enhances nitrogen utilization efficiency. Without sufficient B, N uptake becomes uneven, further aggravating nutrient stress in reproductive tissues.

4. Nutrient-Hormone Interactions and Boll Development

Deficiencies in N, K, and B disrupt hormonal balance in developing bolls:

- +

Hormonal Crosstalk and Regulation Under Stress

1. Abscisic Acid (ABA): The Primary Stress Signal

ABA is the central hormone governing stress responses in cotton, especially under drought and salinity. It promotes stomatal closure to reduce transpiration but also inhibits cell division and reproductive development. Under drought, ABA accumulates in leaves and reproductive tissues, downregulating GA biosynthesis and auxin transport (Müller, 2021). This reduces pollen viability and ovule fertilization. ABA also triggers floral abscission through enhanced ROS production and senescence pathways (Verma *et al*., 2016) [40].

2. Ethylene: A Double-Edged Sword

Ethylene functions as a stress-induced hormone that accelerates senescence and promotes organ abscission. Its overproduction under stress conditions like high temperature and drought can lead to premature boll shedding. Ethylene acts synergistically with ABA to disrupt sink-source balance by promoting programmed cell death in the abscission zones. However, ethylene also plays roles in signaling cascades that initiate antioxidant defenses, making it essential yet potentially harmful when over-accumulated (Souza *et al*., 2017) [38].

3. Auxins and Gibberellins: Growth Sustainers

Auxins (e.g., IAA) and gibberellins support reproductive development by promoting cell division, elongation, and nutrient mobilization. Under stress, their biosynthesis and transport are suppressed by ABA and ethylene (Li *et al*., 2021). Auxin gradients are disrupted under salinity and drought, impairing pollen tube guidance and ovule receptivity. Gibberellins, on the other hand, enhance fiber elongation and boll size but are often antagonized by stress signals. ABA suppresses GA-responsive genes such as GhDREB1, affecting flowering and seed development (Shan *et al*., 2007).

4. Hormonal Crosstalk and Regulatory Balance

Crosstalk between ABA, ethylene, GA, and auxins determines the fate of reproductive organs under stress. Ethylene and ABA often act antagonistically to auxins and GAs, shifting the plant from growth to survival mode (Kumar, 2013) [18]. Hormonal crosstalk also integrates transcription factors such as DREBs, MYBs, and WRKYs, modulating gene expression in bolls. Hormonal ratios (e.g., ABA/GA or IAA/ET) are more critical than absolute concentrations for regulating boll retention (Ross *et al*., 2016).

5. Exogenous Hormone Applications

Studies have shown that foliar sprays of salicylic acid (SA), brassinosteroids (BR), and cytokinins can alleviate stress-induced reproductive losses. For instance, SA enhances ROS-scavenging capacity and stabilizes auxin levels (Kundu & Gantait, 2017) [17]. Brassinosteroids help maintain GA and auxin signaling under heat stress, while paclobutrazol (a GA biosynthesis inhibitor) adjusts hormonal balance under salinity (Forghani *et al*., 2018) [10]. Exogenous ABA has also been tested to induce stomatal closure ahead of stress.

Table 3: Hormonal Changes and Reproductive Outcomes under Abiotic Stresses

Hormone	Stress Type	Change Direction	Reproductive Effect	Reference
ABA	Drought, Salinity	Increase	Stomatal closure, inhibits GA, pollen sterility	Müller (2021), Verma *et al*. (2016) [40]
Ethylene	Heat, Drought	Increase	Floral abscission, boll drop	Pandey *et al*. (2004), Souza *et al*. (2017) [38]
Auxin (IAA)	All	Decrease	Reduced pollen tube growth, ovule abortion	Kundu & Gantait (2017) [17]
Gibberellins	Drought, Cold	Decrease	Impaired seed and fiber development	Shan *et al*. (2007), Li *et al*. (2021)
Brassinosteroids	Heat	Applied ↑	Maintains GA & IAA under heat stress	Li *et al*. (2021)
Salicylic Acid	Heat, Drought	Applied ↑	Enhances ROS detox and reproductive resilience	Kundu & Gantait (2017) [17]

Agronomic Interventions in Enhancing Cotton Stress Tolerance

1. Agronomic Interventions

Abiotic stress tolerance in cotton can be significantly improved through targeted agronomic strategies aimed at minimizing crop exposure to stress, maximizing resource use efficiency, and enhancing physiological resilience. These interventions provide a practical first line of defense, particularly in resource-limited settings.

2. Use of Drought- and Heat-Tolerant Cultivars

Selecting and cultivating stress-tolerant genotypes is among the most direct and impactful agronomic strategies. Genotypes such as 'Suraj', 'LRA-5166', and 'G. cot-13' have shown enhanced drought resilience under Indian field conditions. These cultivars possess traits like deep rooting systems, high relative water content (RWC), efficient stomatal conductance, and superior boll retention under deficit irrigation. Heat-tolerant varieties like 'NHH-44' and 'RCH-134' are increasingly promoted in central and southern India due to their pollen stability and delayed senescence traits.

3. Hormonal Priming and Foliar Nutrition

Hormonal priming refers to the application of growth regulators such as salicylic acid (SA), gibberellic acid (GA), brassinosteroids (BR), and abscisic acid (ABA) in low concentrations to modulate stress responses. For instance, pre-flowering foliar spray of 1.5 mM SA has been shown to enhance flower retention and fiber strength in drought-prone areas. Foliar nutrition with micronutrients (e.g., boron, zinc) is crucial for sustaining pollen viability and ovule development under stress. Potassium nitrate sprays during peak flowering have been demonstrated to improve boll setting and reduce floral shedding under thermal stress by enhancing osmotic balance and maintaining membrane integrity.

4. Crop Scheduling and Planting Techniques

Adjusting planting dates to avoid peak stress periods—particularly heatwaves and late-season droughts—can improve boll retention. Early sowing in semi-arid regions reduces the overlap between flowering and high temperature stress, improving yield. Techniques like ridge and furrow planting, mulching, and drip irrigation enhance water-use efficiency. Ridge sowing enhances root aeration and soil water holding, while mulching reduces evapotranspiration. Drip fertigation systems have shown 30–40% water savings with yield parity or improvement.

5. Soil and Irrigation Management

Soil amendments such as gypsum and organic matter improve salt leaching and root penetration. Integrated nutrient management (INM) involving farmyard manure, compost, and balanced NPK application enhances microbial activity and stress buffering. Deficit irrigation scheduling based on cumulative pan evaporation (CPE) and crop growth stages can reduce water use without sacrificing yield. Cotton irrigated at 0.8 IW/CPE ratio during peak flowering retained more bolls compared to conventional scheduling.

6. Intercropping and Shelterbelt Systems

Intercropping cotton with legumes (e.g., blackgram, cowpea) improves soil structure and nitrogen economy. Shelterbelts using sorghum or maize reduce wind-induced transpiration and heat load on cotton rows, stabilizing microclimate conditions.

Research Gaps and Future Directions

Despite significant laboratory advances in cotton stress physiology research, critical gaps remain in translating findings to field conditions. Most studies employ controlled environments that fail to capture complex soil-plant-microbe interactions, highlighting the need for multi-location trials integrating physiological screening tools like chlorophyll fluorescence and canopy temperature depression. Current research predominantly examines single stresses, while field conditions often present combined stresses (e.g., drought+heat or salinity+nutrient deficiency) that require comprehensive study through factorial experiments and time-series omics data. Emerging technologies like high-throughput phenotyping platforms and systems biology approaches offer promising solutions, particularly when combined with gene co-expression networks and GWAS linked to field performance. Developing climate-resilient cotton demands interdisciplinary collaboration through initiatives like India's AICCIP, incorporating AI/ML models to predict genotype-environment interactions. However, adoption barriers persist, including regulatory hurdles for gene-edited varieties and biofertilizers, necessitating clearer biosafety policies and public-private partnerships. Future efforts should focus on participatory breeding models, decision support systems, and farmer-friendly technologies to bridge the lab-to-field gap and enhance stress resilience in cotton production systems.

Conclusion

The future of cotton resilience lies in harmonizing physiological insights with scalable agronomic and biotechnological interventions. Multi-stress adaptive varieties, supported by precision agriculture tools and regulatory reform, can ensure sustainable cotton production under climate variability.

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