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Impact of abiotic stress on reproductive physiology and boll development in cotton: plant responses and adaptation mechanisms

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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 reproductive physiology, abiotic stresses, boll development, hormonal regulation, nutrient deficiency

Introduction

Cotton (Gossypium spp.), a cornerstone of global agriculture, serves as the primary natural fiber source for textiles while contributing substantially to the oilseed market. Cultivated extensively across tropical and subtropical regions—particularly in India, China, Pakistan, the United States, and Brazil—cotton productivity faces escalating threats from abiotic stresses, including drought, heat, salinity, and nutrient deficiency (Iqbal *et al.*, 2017; Rehman *et al.*, 2021) [18, 33]. These stressors disrupt both vegetative growth and reproductive physiology, leading to reduced boll retention, malformed bolls, and diminished fiber quality (Singh *et al.*, 2018) [38]. At the cellular level, stress triggers membrane destabilization, reactive oxygen species (ROS) accumulation, and hormonal imbalances, which collectively impair photosynthesis and carbohydrate allocation to developing bolls (Zhi *et al.*, 2014; Dalvi *et al.*, 2019) [9, 50]. The reproductive stages—floral induction, anthesis, and boll maturation—are especially vulnerable, as they depend on precise hormonal regulation and stable source-sink relationships (Rehman *et al.*, 2021) [33]. With climate change intensifying these challenges, understanding the physiological and molecular mechanisms of stress tolerance has become critical for sustaining cotton production.

Among abiotic stresses, drought exerts the most severe impact, reducing tissue water potential and impairing turgor-driven cell expansion during boll development (Iqbal *et al.*, 2017) [18]. Water deficit upregulates ABA biosynthesis, triggering stomatal closure and limiting photosynthetic efficiency, while also accelerating floral abscission (Azhar *et al.*, 2018) [1]. Similarly, heat stress above 35°C compromises pollen viability and stigma receptivity, exacerbating boll abortion through ethylene-mediated abscission (Ekinci *et al.*, 2017; Chen *et al.*, 2014) [5, 11]. Salinity stress further compounds these effects by inducing ionic toxicity (Na^+ and Cl^-) and disrupting auxin and gibberellin signaling, which are vital for ovule development (Zhi *et al.*, 2014) [50]. Nutrient deficiencies, particularly boron and potassium, exacerbate reproductive failures by impairing pollen tube growth and osmotic regulation (Dalvi *et al*., 2019) [9]. These stressors collectively disrupt hormonal homeostasis, with elevated ABA and ethylene antagonizing gibberellins and cytokinins—key regulators of flower and boll development (Chen *et al*., 2014) [14]. However, targeted interventions, such as ethylene inhibitors like 1-MCP, demonstrate potential to mitigate stress-induced boll drop, highlighting the centrality of hormonal regulation in reproductive resilience (Chen *et al*., 2014) [5].

To address these challenges, breeding programs are leveraging physiological and molecular traits to develop stress-tolerant cultivars. Traits such as pollen viability, boll retention rate, and cell membrane stability serve as proxies for stress tolerance (Singh *et al*., 2018) [38]. Advances in molecular tools—including QTL mapping, marker-assisted selection, and genome editing—are accelerating the identification of resilience-associated genes, such as *GhCCL*, which enhances boll development under adverse conditions (Dhandapani *et al*., 2014) [8]. A multidisciplinary approach integrating traditional breeding, molecular genetics, and precision agronomy is essential to safeguard cotton's reproductive potential amid climate variability. By unraveling the intricate interplay between stress responses and reproductive physiology, researchers can pave the way for sustainable cotton production in an increasingly unpredictable environment.

Overview of Cotton Reproductive Physiology

Cotton (Gossypium spp.) undergoes a complex series of reproductive events that are intricately regulated by physiological, hormonal, and environmental factors. Understanding the fundamental biology behind floral development, pollination, fertilization, and boll maturation is essential to identifying vulnerable phases influenced by abiotic stress. This section delves into the reproductive timeline of cotton and the source-sink dynamics that underpin successful boll formation and yield realization.

1. Floral Bud Development and Anthesis

Reproduction in cotton is initiated with the formation of floral buds, which arise from the axillary meristems located at the nodes of sympodial branches. These buds begin differentiating approximately 35–40 days after sowing under optimal conditions, with temperature, photoperiod, and hormonal signals influencing their initiation (Oosterhuis, 1990) [24]. Morphologically, the floral bud (commonly called a "square") goes through several developmental stages over a 21–24-day period before blooming. Anthesis marks the opening of the flower, typically occurring in the early hours of the morning and lasting for one day. At this stage, reproductive structures such as stamens (male) and carpels (female) are fully functional. Cotton is primarily self-pollinated, although cross-pollination can occur via insects like bees under field conditions (Mauney, 1986) [22]. During anthesis, pollen is released and deposited onto the stigma, initiating the process of fertilization.

2. Pollination and Fertilization

Pollination in cotton is synchronous with anthesis and involves the transfer of viable pollen grains to the receptive stigma. Pollen tube growth is a rapid and energy-demanding process, guided by chemical cues within the style tissue. Upon reaching the ovule, sperm cells are released to effect double fertilization—one sperm fusing with the egg to form the zygote and the other with central cell nuclei to form the endosperm (Basra, 2000) [2]. Fertilization must occur within a narrow temporal window, generally within 24–48 hours of anthesis, making this phase particularly sensitive to environmental perturbations like drought and heat. Pollen viability and stigma receptivity are highly temperature-dependent; excessive heat (>35°C) can desiccate stigmatic surfaces or denature pollen enzymes, leading to fertilization failure (Singh *et al*., 2018) [38].

3. Embryo and Boll Development

Post-fertilization, embryogenesis and boll development begin. The fertilized ovule develops into a seed, while surrounding tissues give rise to the boll—a protective fruiting structure. Boll development spans approximately 45–55 days and proceeds through three distinct phases: cell division (0–15 DPA, days post-anthesis), cell elongation (15–30 DPA), and secondary wall deposition (30–45 DPA) (Oosterhuis & Jernstedt, 1999) [25]. Each of these stages involves specific metabolic and structural changes that require robust physiological support. During the elongation phase, fiber cells can grow up to 3 cm in length, driven by turgor pressure and regulated by the activity of expansins, aquaporins, and enzymes like cellulose synthase (Haigler *et al*., 2001) [17]. Water availability and hormonal equilibrium (e.g., auxin and gibberellin) are key to these growth processes.

4. Boll Maturation and Opening

As the fiber development transitions to the thickening stage, large amounts of carbohydrates are transported into the bolls for cellulose biosynthesis. Mature bolls eventually dehisce, or open, exposing the lint for mechanical or manual harvesting. The boll opening phase is influenced by declining auxin levels and increased ethylene production, which facilitates cell wall loosening in the carpel tissues (Chen *et al*., 2014) [5]. Boll retention and size are critical determinants of final yield. Even a minor disruption during this stage—due to stress, hormonal imbalance, or pest attack—can lead to boll shedding or incomplete fiber development (Iqbal *et al*., 2017) [18].

5. Source-Sink Dynamics in Reproductive Growth

The source-sink relationship refers to the balance between assimilate-producing tissues (sources, mainly mature leaves) and assimilate-consuming organs (sinks, such as bolls). During reproductive development, cotton's metabolic priority shifts heavily toward sink organs. Sucrose and other photoassimilates are translocated via the phloem from leaves to developing bolls, especially during the peak boll filling stage. Stress conditions such as drought or nutrient limitation can inhibit photosynthesis or phloem transport, thereby reducing assimilate availability for boll development. This phenomenon, termed "sink limitation," results in reduced boll size, fiber maturity index, and seed weight (Azhar *et al.*, 2018) [1]. Furthermore, carbohydrate allocation is regulated by hormonal gradients. For example, cytokinins promote cell division in the early boll stage, while gibberellins and auxins are vital for elongation and expansion. ABA accumulation under stress reduces sink strength by promoting leaf senescence and stomatal closure, which restricts photosynthetic carbon fixation (Haigler *et al.*, 2001; Singh *et al.*, 2018) [17, 38].

6. Hormonal Regulation During Reproduction

Plant hormones play an orchestrated role in guiding reproductive development. Auxins (IAA), cytokinins, gibberellins (GA), abscisic acid (ABA), and ethylene are the key players.

- **Auxins** are essential during floral initiation, ovule development, and early boll formation. They help maintain sink strength and prevent premature abscission by suppressing ethylene sensitivity (Oosterhuis, 1990) [24].
- **Cytokinins** influence cell division and ovule formation. A reduction in cytokinins under stress has been linked to reduced boll set.
- **Gibberellins** support cell elongation and fiber growth but are highly sensitive to water availability.
- **Abscisic acid (ABA)** is a central stress-responsive hormone. Elevated ABA levels under drought and salinity contribute to boll shedding by interacting antagonistically with growth-promoting hormones.
- **Ethylene**, when induced under heat or drought, accelerates floral and boll abscission (Chen *et al.*, 2014) [5].

Exogenous applications of hormonal antagonists such as 1-methylcyclopropene (1-MCP), which blocks ethylene receptors, have been shown to enhance boll retention and lint yield under stress conditions (Chen *et al.*, 2014) [5].

7. Anatomical and Molecular Basis of Reproductive Organ Sensitivity

The reproductive tissues of cotton are anatomically predisposed to stress sensitivity. The large vacuolated cells of developing fibers, the thin-walled stigma cells, and the vascular connections to the bolls are highly dependent on water status and turgor pressure. Furthermore, molecular studies have identified stress-responsive genes such as GhDREB, GhHSP, and GhCCL that are upregulated in reproductive tissues under abiotic stress, providing insights into intrinsic defense mechanisms (Dhandapani *et al.*, 2014) [8]. Despite this, reproductive organs often lag behind vegetative tissues in acquiring full stress tolerance. This is due to differential gene expression, limited cuticular protection, and the metabolic cost associated with gamete development and fertilization.

Drought Stress and Reproductive Failure in Cotton

Drought stress is one of the most pervasive abiotic constraintas in global cotton cultivation, with severe consequences for reproductive development and yield realization. The following section elaborates the physiological, biochemical, and hormonal disruptions caused by drought stress, highlighting how they converge to induce reproductive failure.

1. Impact on Floral Bud Initiation

Floral bud initiation in cotton is a highly energy-demanding process that relies on sustained water availability, photosynthate production, and hormonal coordination. Under drought conditions, reduced soil moisture leads to a drop in turgor pressure and impaired cell expansion in the shoot apical meristem, thereby inhibiting the transition from vegetative to reproductive growth (Saleem *et al.*, 2015) [42]. This physiological bottleneck results in fewer floral buds (squares), delayed flowering, and ultimately reduced fruiting sites. Furthermore, water stress affects cytokinin transport from roots to shoots, a hormone known to promote meristematic activity and floral initiation. The decline in cytokinin levels under drought impairs cell division in apical tissues, stunting floral development and decreasing the number of fruiting sites (Padmalatha *et al.*, 2012; Zhang *et al.*, 2016) [30, 49].

2. Pollen Viability and Fertilization Disruption

One of the most drought-sensitive stages of cotton reproduction is pollen development and viability. Studies indicate that 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]. Moreover, lower activity of enzymes such as ADP-glucose pyrophosphorylase and α-amylase under drought conditions further impairs starch biosynthesis and breakdown, starving the growing pollen tube of essential ATP and carbon skeletons (Hu *et al.*, 2019) [14]. Pollen tube elongation is thus slowed, reducing the probability of successful ovule fertilization. A parallel study by Zare *et al.* (2014) confirms that drought-induced oxidative stress leads to membrane lipid peroxidation in pollen grains, further reducing their viability. High levels of reactive oxygen species (ROS) under drought conditions damage nucleic acids and cellular membranes in gametophytic tissues, contributing to male sterility.

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]. Furthermore, 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 was observed, resulting 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. This reflects in smaller, poorly filled bolls and reduced lint percentage.

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) [34]. 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) [31]. 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) [30].

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) [18]. 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) [5]. 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) [5].

Table:1 Impacts of Drought on Cotton Reproduction

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) [30, 42]
Pollen viability	↓ 30–60% in drought-sensitive genotypes	Disrupted carbohydrate metabolism, oxidative stress	Hu *et al*. (2019) [14]; Zare *et al*. (2014)
Ovule fertilization	Reduced fertilization success	Sucrose accumulation; low ATP in pistils	Hu *et al*. (2019) [14]; Hu *et al*. (2020) [15]
Boll set and retention	Boll shedding increased by 40–70%	Ethylene production; carbohydrate shortage	Pilon (2014); Chen *et al*. (2014) [5, 31]
Photosynthetic rate	Declines 30–50% within 7–10 days of stress onset	ABA-induced stomatal closure	Rahman *et al*. (2008) [34]
Sugar translocation to bolls	Reduced by 50% in stressed plants	Impaired phloem loading, lower sucrose synthase activity	Padmalatha *et al*. (2012) [30]
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) [40]. 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) [19]. Similar reductions were reported by Song *et al*. (2015) [41], 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) [40].

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) [19].

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) [20]. 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. Burke *et al*. (2004) [4] found that optimal germination occurs between 28–31 °C, while rates plummet at

37 °C and are nearly eliminated by 39 °C. High temperature also impairs pollen tube growth, decreasing fertilization potential (Song *et al*., 2015) [41].

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) [44] 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) [19]. These proteins assist in maintaining 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) [33] 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*. (2018) [38] 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) [10]. 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) [37]. 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.

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) [36]. 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) [37]. 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) [43] 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) [36].

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) [37]. 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.

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) [45]
3.10	32 Indian upland varieties	3.5	85	8.7	Dinakaran *et al*. (2012) [10]
4.0	LH 1556	3.2	78	8.1	Sharma & Brar (2005) [37]
6.0	Bikeneri Nerma	2.8	72	7.5	Bhute *et al*. (2012) [3]
8.0	PH 1009 (stress-tolerant)	2.6	68	7.2	Yadav (2015) [45]
9.0	Upland cotton meta-analysis	2.2	60	6.4	Paknejad *et al*. (2020) [29]
10.5–11.0	CCRI-79 (tolerant) + K applied	3.0	70	7.8	Ju *et al*. (2021) [12]

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) [13]. Studies have shown that low N levels reduce the number of bolls per plant, boll size, and boll weight. Yuan *et al*. (2018) 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. Read *et al*. (2006) [32] observed reductions in glutamine synthetase (GS) and glutamate synthase (GOGAT) activity under N stress, further affecting nitrogen assimilation and boll filling.

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) [27]. Hu *et al*. (2016) [16] 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, Parmar (2006) [26] 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) [28] 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. Miley *et al*. (1969) [21] found that boron-deficient plants showed increased ringed petioles and aborted floral buds. 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 (Miley *et al*., 1969).

4. Nutrient-Hormone Interactions and Boll Development

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

- **Low N** reduces cytokinin and auxin levels, weakening sink strength.
- **Low K** enhances ethylene synthesis, promoting boll abscission.
- **Low B** inhibits auxin transport and impairs calcium mobility, destabilizing ovule development.

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).

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 (Pandey *et al*., 2004). Ethylene acts synergistically with ABA to disrupt sink-source balance by promoting programmed cell death in the abscission zone. 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).

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). 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). 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). 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)
Ethylene	Heat, Drought	Increase	Floral abscission, boll drop	Pandey *et al*. (2004), Souza *et al*. (2017)
Auxin (IAA)	All	Decrease	Reduced pollen tube growth, ovule abortion	Kundu & Gantait (2017)
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)

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.

8.1 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.

2. 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.

3. 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.

4. 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.

5. 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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