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The role of phytohormones in regulating growth and reproductive development in maize (*Zea Mays* L.): Insights into stress resilience and yield stabilization

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Abstract

The growth and reproductive development of maize (*Zea Mays* L.) are intricately regulated by a complex interplay of phytohormones, including auxins, gibberellins (GAs), cytokinins (CKs), abscisic acid (ABA), ethylene, salicylic acid (SA), jasmonic acid (JA), and brassinosteroids (BRs). These hormones play crucial roles in key physiological transitions, from germination and root–shoot axis establishment to flowering, pollination, and kernel development, by modulating gene expression, enzyme activity, and stress responses. This comprehensive review examines the spatiotemporal roles of these hormones at different developmental stages, with a focus on their interactions (crosstalk), feedback mechanisms, and fluctuations under stress conditions. The review highlights how hormonal imbalances under abiotic stress (drought, salinity, heat, and oxidative damage) can impair reproductive success by affecting pollen viability, stigma receptivity, ovule fertilization, and grain filling. It also explores agronomic and biotechnological interventions, such as exogenous hormone applications, hormone priming, and integration into crop management systems. Additionally, the paper discusses emerging research tools, including QTL mapping, transcriptomics, and hormone diagnostics, which are essential for precision breeding of stress-resilient maize cultivars. These insights provide a deeper understanding of how targeted hormonal regulation can enhance maize productivity in the face of climate variability.

Keywords: Maize physiology, plant hormones, reproductive development, abiotic stress, auxin, gibberellin, cytokinin, aba, brassinosteroids, hormone priming, grain yield, stress tolerance

Introduction

Maize (*Zea Mays* L.), a globally significant C4 cereal crop, exhibits remarkable responsiveness to its internal hormonal balance throughout all developmental stages, ranging from seed germination and seedling vigor to reproductive organ development and grain filling. The intricate orchestration of plant growth regulators or phytohormones—such as auxins, gibberellins (GAs), cytokinins (CKs), abscisic acid (ABA), ethylene, jasmonates (JAs), and brassinosteroids (BRs)—is fundamental to the physiological integrity and reproductive success of maize. In the current context of escalating abiotic stress scenarios driven by climate variability, hormonal regulation has emerged as a pivotal determinant of yield stability in maize. Plant hormones function as low-concentration signaling molecules that coordinate cellular activities and developmental transitions. The complex interplay, or crosstalk, between growth-promoting hormones (e.g., auxins, GAs, CKs) and stress-responsive regulators (e.g., ABA, ethylene, SA) governs processes such as root architecture modulation, meristem maintenance, inflorescence development, and seed maturation. For instance, auxin transport via PIN proteins regulates organ polarity and floral organogenesis, while cytokinin-mediated signaling influences spikelet formation and reproductive meristem activity (Yang & Li, 2012) [41]. The transition from vegetative to reproductive growth in maize is marked by a tightly regulated hormonal balance, particularly involving gibberellins and auxins. Gibberellins promote flowering and tassel elongation, while a drop in ABA levels facilitates floral transition (Chen *et al*., 2014) [9]. Auxin also plays a role in floral meristem identity, with mutants in auxin biosynthesis or response pathways resulting in malformed tassels and ears (Phillips, 2009) [23]. During the reproductive stage, hormonal coordination becomes increasingly vital. Cytokinins are enriched in sink tissues such as developing kernels, where they delay senescence and enhance cell division. ABA levels rise post-pollination, playing a central role in grain filling and maturation. However, under drought or salinity stress, premature ABA accumulation can accelerate senescence and reduce kernel set, highlighting its dual role depending on timing and concentration (Wang, 2014) [37]. The action of ethylene, often labeled as a stress hormone, further complicates reproductive development. While ethylene regulates silk senescence and the timing of pollination, elevated levels under heat or drought stress can disrupt ovule fertilization and enhance floral abortion (Mehri, 2015) [20]. Therefore, precise hormonal tuning, both endogenous and via exogenous application, becomes critical to sustain yield. Brassinosteroids, a relatively recent addition to the hormone family, are now understood to enhance reproductive performance under stress by maintaining pollen viability and supporting starch synthesis during grain development. Their interaction with GAs and auxins reinforces cellular expansion and resource allocation to reproductive organs (Kim *et al*., 2004). The application of exogenous hormones such as GA_3, cytokinin, salicylic acid (SA), and brassinosteroids has been explored in numerous field and controlled studies. These applications have demonstrated notable impacts on yield parameters, including increased ear length, grain number, and harvest index, especially under drought or nutrient-deficient conditions (Akter *et al*., 2014).

These findings indicate the growing interest in hormonal manipulation as a pragmatic tool in crop management.

This review systematically examines the role of key plant hormones in regulating vegetative and reproductive development in maize. Beginning with seedling establishment and progressing through inflorescence formation, pollination, fertilization, and grain development, each stage will be evaluated in terms of its hormonal drivers. Special focus will be given to:

- The individual and combined effects of phytohormones on reproductive physiology;
- Hormonal interplay during abiotic stress and its impact on fertility and yield;
- Field-level evidence of hormonal interventions through foliar sprays or seed priming;

This comprehensive synthesis aims to provide researchers, crop physiologists, and agronomists with a consolidated understanding of how plant growth hormones govern the productivity trajectory of maize, highlighting both physiological insights and translational opportunities in crop improvement.

Hormonal Regulation of Vegetative Growth in Maize

1. Seed Germination and Seedling Vigor

Maize seed germination is a complex physiological process regulated by a network of hormones, including gibberellins (GAs), abscisic acid (ABA), and auxins. This stage is critical as it marks the transition from a dormant embryo to an actively growing seedling, setting the stage for crop establishment and yield potential. Gibberellins are central to germination physiology, particularly in monocots like maize. GAs stimulate the synthesis of hydrolytic enzymes, especially α-amylase, in the aleurone layer, which helps mobilize the starch reserves stored in the endosperm. This energy supply is essential for radicle protrusion and mesocotyl elongation. In developing maize kernels, GA biosynthesis precedes ABA accumulation, establishing a favorable GA/ABA ratio necessary for germination. Disruption of GA biosynthesis, either through genetic mutations or chemical inhibitors, results in delayed or suppressed germination, underscoring GA's critical role.

Conversely, ABA acts as the primary inhibitor of seed germination. In maize, ABA maintains dormancy during late embryogenesis and imposes desiccation tolerance, preventing premature sprouting (vivipary) under unfavorable conditions (Ali *et al*., 2021) [2, 3]. The antagonistic interaction between GA and ABA acts as a regulatory switch: a high ABA/GA ratio preserves dormancy, while a reduced ratio triggers germination. Maize mutants such as viviparous5 (vp5), which are deficient in ABA biosynthesis, exhibit precocious germination on the cob, highlighting ABA's suppressive role. Auxin, although traditionally associated with post-germination growth, also plays a nuanced role during seed dormancy and germination. Recent findings suggest that elevated auxin levels can reinforce dormancy by upregulating ABA biosynthesis and downregulating GA pathways, effectively decreasing the GA/ABA ratio (Shuai *et al*., 2017) [29]. Auxin delays seed coat rupture and radicle emergence by modulating cell wall loosening enzymes and hormonal balance.

In early seedling development, auxin facilitates root meristem activation, radicle elongation, and mesocotyl expansion through differential gene expression and asymmetric distribution via PIN transporters. These responses enhance seedling vigor, particularly under suboptimal conditions like compacted soils or temperature stress (Wu *et al*., 2020) [40].

2. Root–Shoot Axis Development

Following germination, hormonal gradients direct the architectural development of the primary root, shoot apex, and lateral organs. Auxins and cytokinins play dominant, yet often antagonistic, roles in patterning the root–shoot axis.

Auxin accumulation at the root tip is essential for establishing and maintaining root apical meristem (RAM) activity. It promotes cell division in the quiescent center and orchestrates differentiation in the elongation zone. Polar auxin transport, regulated by PIN and AUX/LAX proteins, ensures the spatial specificity of auxin maxima necessary for initiating lateral roots and defining root architecture. In contrast, cytokinins accumulate preferentially in the shoot apical meristem (SAM), where they stimulate cell proliferation and leaf primordia initiation. Their inhibitory action on root elongation is exerted via type-B ARR signaling, which downregulates PIN expression and disrupts auxin flow. This classic auxin-cytokinin antagonism delineates organ identity: auxin favors root growth, while cytokinin supports shoot development.

The maize vp10 mutant, which is defective in molybdenum cofactor synthesis, simultaneously displays deficiencies in both ABA and auxin levels, leading to poor root development and seedling lethality. This further underscores the interdependence of hormonal networks in supporting vegetative growth. Auxin-ABA interactions also govern root plasticity under stress. ABA represses lateral root formation via auxin redistribution and suppression of local auxin response elements. In maize, stress-responsive root architecture is modulated by hormonal ratios rather than absolute hormone concentrations, reinforcing the need for dynamic hormonal interplay (Shu *et al*., 2016) [28].

Table 1: Physiological Effects of Hormone Treatments on Maize Seedlings

Hormone Treatment	Germination %	Root/Shoot Ratio	Chlorophyll Index	Reference(s)
GA (100 ppm)	95%	1.4	High	Akter *et al*. (2014)
ABA (50 µM)	30%	0.8	Low	Ali *et al*. (2021);
Auxin (IAA, 10 µM)	55%	1.1	Moderate	Shuai *et al*. (2017) [29]. Wu *et al*. (2020) [40].
GA + Auxin	85%	1.3	High	Wu *et al*. (2020) [40].
ABA + Auxin	20%	0.7	Very Low	Shu *et al*. (2016) [28].

Hormonal Regulation of Transition to Reproductive Phase

1. Gibberellins as Primary Signals in Floral Induction

As a plant physiologist, I find it fascinating how gibberellins (GAs) play a crucial role in steering maize from vegetative growth to reproductive development. Unlike Arabidopsis, which has multiple pathways influencing flowering, maize relies heavily on GAs to orchestrate internode elongation, shifts in meristem identity, and the initiation of floral meristems. For instance, GA-deficient maize mutants such as dwarf1, dwarf3, and anther ear1 show significant delays in transitioning to the reproductive phase and exhibit morphological anomalies in reproductive organs. This underscores the necessity of bioactive GAs for the proper development of tassels and ears.

GAs act downstream of the GA20ox and GA3ox genes, which are pivotal in catalyzing the final steps of GA biosynthesis. During floral induction, GAs boost the expression of key floral integrator genes, including LEAFY (LFY), SUPPRESSOR OF CONSTANS1 (SOC1), and FLOWERING LOCUS T (FT)-like genes, especially under long-day conditions (Mutasa-Göttgens & Hedden, 2009) [22]. In maize, GAs also facilitate the vegetative phase change by suppressing juvenile traits (e.g., epicuticular wax) and enhancing adult leaf characteristics before floral initiation. The GA-responsive microRNA miR159 further fine-tunes these transitions by targeting GAMYB transcripts, which are involved in regulating LFY and anther development.

2. Integration of Photoperiod and Hormonal Pathways

Maize, being ancestrally a short-day (SD) plant, has a tightly regulated system where photoperiodic signals and hormonal responses work in tandem to control flowering. FT-like genes, such as ZCN8, act as mobile florigenic signals that are activated under SD conditions. These signals are transported from leaves to the shoot apical meristem (SAM), where they trigger downstream targets essential for floral transition (Meng *et al*., 2011) [21]. GA biosynthesis is also ramped up under inductive photoperiods through the upregulation of GA20ox gene expression in leaf tissues. In photoperiod-sensitive maize lines, GA levels and ZCN8 expression are rhythmically regulated, highlighting the intricate link between daylength cues and endogenous signals. Experimental evidence indicates that GA stimulates ZCN8-mediated activation of floral meristem identity genes at the SAM, effectively bridging environmental inputs with hormonal promotion of flowering (Marciniak *et al*., 2017) [19].

3. Ethylene's Role Under Sub-Optimal Conditions

Ethylene, often labeled as a stress hormone, has a dual role in floral development. Under optimal conditions, it helps fine-tune the timing of flower initiation and stigma receptivity. However, under sub-optimal environments like heat stress, drought, or low nutrient availability, elevated ethylene levels can be detrimental to reproductive development. For example, heat-induced ethylene biosynthesis can accelerate senescence and trigger ovule abortion and floral drop, especially during early reproductive stages. In maize, heightened ethylene production is linked to shortened anthesis-silking intervals (ASI), reduced pollen viability, and impaired ovule fertilization, ultimately leading to decreased kernel set and overall yield (Stephenson *et al*., 2018) [31].

The interplay between ethylene and GA is particularly critical during stress. Ethylene can modulate DELLA proteins, which are repressors of GA signaling. Under heat or salinity, increased ethylene levels lead to the accumulation of DELLA proteins, thereby suppressing GA-mediated floral induction pathways. This antagonism is exemplified in the gai eto2-1 double mutant in Arabidopsis, where decreased GA sensitivity combined with elevated ethylene biosynthesis results in delayed flowering and floral organ deformation (De Grauwe *et al*., 2007) [13]. This hormonal crosstalk also impacts photoperiodic flowering. Ethylene has been observed to alter FT expression in cotyledons and leaves, thereby interfering with the florigenic signal transport. In photoperiod-sensitive systems, ethylene overproduction can delay flowering or even revert inflorescence initiation, contributing to floral sterility under adverse field.

Reproductive Development: Hormone-Driven Processes in Maize

Reproductive success in maize (*Zea Mays* L.) hinges on a complex hormonal framework. This section delves into the physiological roles of phytohormones at critical stages of reproductive development, including tassel and ear formation, silk emergence and receptivity, pollination and fertilization, and kernel development.

1. Hormonal Regulation of Tassel and Ear Development

Gibberellins (GAs), cytokinins (CKs), and auxins are pivotal in regulating tassel and ear morphogenesis. Tassel development necessitates the timely initiation of male floral meristems from the shoot apical meristem, a process modulated by GAs that promote elongation and maturation of the floral axis (Yu *et al*., 2016) [42, 43]. Deficiencies in GA biosynthesis genes, such as anther ear1 and dwarf1, result in underdeveloped tassels and delayed floral organogenesis. Conversely, CKs support meristem maintenance and branching, which is crucial for determining tassel architecture. Mutants with enhanced CK activity, like abph1, exhibit enlarged inflorescences due to increased meristem size (Thompson, 2014) [33, 34]. In the developing ear, auxins promote the initiation of floral primordia and vascular connectivity. Nitrogen limitation, which alters the auxin and GA balance, leads to shorter ears with fewer kernels, often accompanied by hormonal imbalances (upregulation of IAA14, GA2ox1, CKX12) and early senescence (Yu *et al*., 2016) [42, 43].

2. Silk Growth and Stigma Receptivity

Silk emergence and elongation are crucial for successful pollination. This phase is tightly regulated by auxins, GAs, and brassinosteroids. Auxins stimulate cell expansion and elongation of silk tissues, while GAs coordinate tissue elongation and stigma development. A deficit in these hormones under stress conditions, such as drought or shading, severely impairs silk growth. Silk receptivity, defined as the ability to support pollen adhesion, germination, and tube growth, declines rapidly after emergence. Ethylene and ABA accelerate silk senescence, while delayed pollination or environmental stress reduces the functionality of silks (Bassetti & Westgate, 1993) [6].

3. Pollination and Fertilization Dynamics

Pollination success depends on hormone-mediated coordination between tassel-derived pollen and ear-derived silks. Jasmonic acid (JA) and auxins regulate pollen viability and tube elongation. Stress-induced hormonal imbalances disrupt this synchrony. High temperature, for instance, causes pollen sterility via ethylene accumulation and impaired GA-JA signaling. Heat-stressed tassels produce fewer and morphologically deformed pollen grains, reducing successful fertilization events. Delayed or asynchronous pollination also negatively affects kernel number per ear. Synchronous pollination improves kernel set and pollen utilization, suggesting a hormonal window for optimized reproductive synchrony (Cárcova *et al*., 2000).

4. Hormonal Control of Kernel Development

Post-fertilization, kernel development is hormonally orchestrated to allocate resources and sustain embryogenesis. CKs are elevated in the endosperm and support cell division. ABA regulates the transition from cell proliferation to maturation, while auxin enhances assimilate flow into developing grains. Shading or nutrient stress reduces IAA and CK content while increasing ABA, leading to grain abortion. Exogenous application of CKs and auxins at early grain filling stages mitigates these effects by prolonging sink activity and improving kernel retention (Davis, 2009) [12].

Table 2: Key Hormones Involved in Maize Reproductive Development and Their Roles

Stage	Key Hormones	Functional Role	Stress Sensitivity	Key References
Tassel & Ear Formation	GA, CK, Auxin	Meristem development, floral initiation	High (under N-deficiency, heat)	Yu *et al.* (2016) [42, 43], Thompson (2014) [33, 34].
Silk Growth & Receptivity	Auxin, GA, Ethylene	Silk elongation, pollen adhesion and germination	High (under drought, heat)	Bassetti & Westgate (1993) [6].
Kernel Development	CK, ABA, Auxin	Endosperm proliferation, starch biosynthesis, grain filling	Moderate to high (shading, nutrient stress)	Davis (2009) [12].

Pollination, Fertilization, and Kernel Set: Hormonal Regulation in Maize

1. Hormonal Regulation of Pollen Viability and Germination

1.1 Role of Auxins in Pollen Maturation

Auxins, particularly indole-3-acetic acid (IAA), are essential for pollen development. They regulate tapetum function, microspore maturation, and starch accumulation in pollen grains. Auxin biosynthesis genes, such as YUCCA, are highly expressed in developing anthers. Auxin-deficient lines show malformed or non-viable pollen (Cecchetti *et al.*, 2017) [11].

1.2 Jasmonic Acid and Pollen Function

Jasmonic acid (JA) is crucial for late anther development and pollen viability. It induces the expression of genes associated with pollen coat formation and programmed cell death in tapetal cells. JA-deficient mutants (opr3) exhibit male sterility in maize due to poor pollen germination and tube elongation.

1.3 Crosstalk Between Auxin and JA

JA and auxin synergistically promote pollen hydration and germination on the silk. This hormonal integration also impacts the ROS signaling pathways and enhances callose degradation, facilitating pollen tube penetration (Zhao *et al.*, 2020) [1, 49, 50].

2. Hormonal Control of Pollen Tube Growth and Ovule Receptivity

2.1 Gibberellins and Pollen Tube Elongation

Gibberellins (GAs) stimulate pollen tube elongation by promoting cell wall loosening enzymes (expansins, pectinases) and calcium influx. GAs also upregulate actin polymerization and vesicle transport needed for tip growth (Singh *et al.*, 2014) [30].

2.2 ABA and Stigma Senescence Under Stress

Abscisic acid (ABA) levels rise under heat and drought stress, leading to premature stigma senescence and reduced receptivity. ABA suppresses aquaporin expression and reduces stigma hydration capacity, impeding pollen adhesion (Zhang *et al.*, 2019) [47].

2.3 Hormonal Synchrony and Fertilization Success

Successful fertilization requires temporal synchrony between pollen tube arrival and ovule viability. Disruption in auxin-GA-ABA balance affects embryo sac longevity and impairs double fertilization. Treatments with exogenous GA or auxin partially restore seed set under stress (Ali *et al.*, 2020) [1].

3. Ethylene and Kernel Abortion Under Abiotic Stress

3.1 Ethylene as a Stress-Induced Signal

Under combined drought and heat, ethylene biosynthesis accelerates in silks and ovules. Ethylene inhibits cell division in zygotic tissues and promotes programmed cell death, leading to ovule abortion (Wang *et al.*, 2016) [39].

3.2 Interaction with ABA and ROS Pathways

Ethylene interacts with ABA and reactive oxygen species (ROS), exacerbating oxidative damage in reproductive tissues. This results in poor kernel filling and reduced grain number (Farooq *et al.*, 2011) [15].

3.3 Mitigation Strategies: Hormonal Priming

Application of ethylene inhibitors (e.g., AVG or silver thiosulfate) and hormone priming with BRs or SA under stress conditions has been shown to reduce kernel abortion and improve reproductive success (Zhao *et al.*, 2018) [48].

Hormonal Control of Grain Filling and Maturation

1. Cytokinins and Endosperm Sink Strength

Cytokinins play a central role in enhancing endosperm cell division and delaying senescence, thereby prolonging the grain-filling period. Elevated levels of CKs such as zeatin and zeatin riboside in the endosperm promote cell proliferation and enhance sink strength by upregulating genes involved in nutrient transport and starch synthesis (Wei *et al.*, 2019). In Indian field studies, foliar application of benzyladenine (BA), a synthetic cytokinin, during the early grain-filling stages significantly improved kernel number and size by increasing endosperm cell division (Qing, 2015) [24]. Disruption in CK levels due to environmental stress (e.g., heat or drought) leads to a premature decline in sink strength and reduced grain filling. Exogenous CK application has been shown to counteract this by maintaining higher zeatin levels and chlorophyll content in leaves, preserving photosynthetic activity (Cheikh & Jones, 1994) [8].

2. ABA Regulation of Maturation and Stress Response

ABA functions as a maturation signal during late grain filling. It regulates the expression of late embryogenesis abundant (LEA) proteins, enhances starch accumulation, and promotes desiccation tolerance in maturing kernels (Zhang *et al.*, 2018) [46]. Elevated ABA levels during stress hasten maturation and dehydration, sometimes at the cost of yield. A study from China demonstrated that drought-induced ABA triggers early activation of sucrose-metabolizing enzymes such as sucrose synthase and ADP-glucose pyrophosphorylase, accelerating grain dehydration and starch synthesis (Jiang *et al*., 2021) [17]. In an Indian study, ABA accumulation was linked with early cessation of grain filling in stressed environments. However, co-application with CKs buffered this effect, maintaining grain-filling duration and improving kernel dry weight (Yang *et al*., 2001).

3. Brassinosteroids and Assimilate Allocation

Brassinosteroids (BRs) regulate grain filling by enhancing photosynthetic efficiency, source-to-sink translocation of assimilates, and starch biosynthesis in the endosperm. BRs upregulate key enzymes including PEP carboxylase, RuBP carboxylase, and sucrose synthase in the ear leaf, thus increasing the availability of photosynthates for the developing grain. Studies have shown that BR application during early to mid grain filling significantly improves chlorophyll retention, grain weight, and kernel starch content under both optimal and suboptimal conditions (Zhang *et al*., 2011) [44].

Table 3: Correlation Between Kernel Growth Rate and Cytokinin/ABA Levels in Endosperm Tissues

Kernel Growth Phase	CK Level (µg/g FW)	ABA Level (µg/g FW)	Kernel Growth Rate (mg/day)	Key Observations	Reference(s)
Early (7–14 DAP)	3.5	1.1	2.8	High cell division, strong sink formation	Wei *et al*. (2019), Qing (2015) [24].
Mid (15–21 DAP)	2.8	2.9	3.4	Peak sucrose import, active starch synthesis	Zhang *et al*. (2018) [46], Jiang *et al*. (2021) [17].
Late (22–30 DAP)	1.2	4.8	1.9	ABA-driven desiccation and maturation	Yang *et al*. (2001)

Hormonal Dynamics Under Abiotic Stress

1. Abscisic Acid (ABA): The Core Stress Hormone

ABA plays a central role in mediating stress responses by regulating stomatal closure, osmolyte accumulation, and gene expression. Under drought or salinity, rapid ABA biosynthesis via NCED genes leads to stomatal closure and ROS production, preserving cellular water (Ma *et al*., 2018). ABA also induces LEA proteins and other dehydrins that protect reproductive tissues during desiccation. Transcriptome studies show that drought-induced ABA modulates the expression of over 200 stress-related genes (Rehman *et al*., 2021) [25].

2. Ethylene: A Double-Edged Sword

Ethylene's role under stress is dualistic. While low levels promote defense gene expression, excessive ethylene (especially under drought–heat combinations) accelerates floral abscission and ovule abortion (Haider *et al*., 2021) [16]. Ethylene and ABA often act antagonistically. Ethylene promotes ROS-mediated senescence, while ABA protects against it. Elevated ethylene disrupts GA biosynthesis, thereby reducing pollen tube growth and kernel set.

3. Salicylic Acid (SA) and Hormonal Buffering

SA enhances tolerance to salinity and oxidative stress by upregulating antioxidant enzymes. SA mitigates ethylene overproduction and stabilizes photosynthetic machinery under high light and temperature. Exogenous SA application during anthesis improves pollen viability and reduces silk desiccation (Ali & Malik, 2021) [2, 3]. SA also regulates crosstalk with JA and ABA pathways to balance defense and reproductive growth (Wang *et al*., 2021) [38].

4. Brassinosteroids (BRs) in Stress Tolerance

BRs enhance grain filling and stress tolerance by promoting chlorophyll retention and antioxidant enzyme activities. BRs interact with ABA and SA signaling to fine-tune stress-responsive transcription factors (e.g., DREB, HSFs) (Zhang *et al*., 2013) [45]. Application of BR analogs during flowering and grain-filling stages improves kernel weight under drought and salinity.

5. Auxin and Gibberellin Perturbation Under Stress

Drought and salinity downregulate auxin transporters (PINs), disrupting root development and silk elongation. GA signaling is inhibited by high ABA and ethylene, leading to arrested reproductive growth (Shan *et al*., 2013) [27]. Stress-induced DELLA accumulation represses GA activity, reducing tassel branching and ear size.

6. Strigolactones and Hormone Crosstalk

Strigolactones (SLs) increase under nutrient and water limitations. They regulate stomatal density and interact with auxins and CKs to optimize root and shoot growth under stress (Bhoi *et al*., 2021) [7]. SL-ABA and SL-GA interactions help fine-tune developmental responses under fluctuating environments.

Table 4: Comparative Hormonal Shifts Under Abiotic Stresses and Their Effects on Maize Reproduction

Stress Type	Key Hormonal Changes	Crosstalk Effects	Reproductive Consequences	Reference(s)
Drought	↑ ABA, ↑ ET, ↓ Auxin, ↓ GA	ABA–ET antagonism, ABA–CK buffering	Silk desiccation, kernel abortion	Ma *et al*. (2018); Rehman *et al*. (2021) [25].
Heat	↑ ET, ↑ ABA, ↓ JA	ET-induced senescence, ABA–BR mitigation	Pollen sterility, stigma collapse	Haider *et al*. (2021); Wang *et al*. (2021) [16, 38].
Salinity	↑ ABA, ↑ SA, ↓ GA	ABA–SA synergy, GA–ET suppression	Reduced silk growth, ovule abortion	Bhoi *et al*. (2021) [7].
Cold	↑ ABA, ↓ Auxin	ABA–GA antagonism	Delayed pollination, low fertilization	Shan *et al*. (2013) [27].
Oxidative	↑ SA, ↑ JA	JA–SA synergy, ROS–ABA feedback	Enhanced antioxidant defense, pollen survival	Wang *et al*. (2021); Ali & Malik (2021) [2, 3, 38].

Application of Exogenous Hormones in Crop Management

The exogenous application of phytohormones such as gibberellic acid (GA_3), salicylic acid (SA), and brassinosteroids (BRs) has emerged as a powerful agronomic intervention to enhance abiotic stress resilience in maize. These growth regulators influence plant metabolism, reproductive success, and grain yield by modulating physiological and molecular responses during critical growth stages. This section synthesizes findings from field trials and case studies evaluating hormone applications in maize under diverse environmental conditions.

1. Foliar Applications for Enhancing Stress Tolerance

Field trials conducted across South Asia and the Middle East demonstrated that foliar SA applications (100–300 mg L^{-1}) significantly improved maize tolerance to drought and salinity stress by enhancing chlorophyll content, antioxidant enzyme activity, and relative water content (Al Rawi *et al*., 2021) [4]. The best results were seen when SA was applied at V6 (6-leaf) and tasseling stages. In a separate study, foliar application of BR (0.5–1.0 mg L^{-1} epibrassinolide) increased maize tolerance to water stress by stimulating photosynthetic activity and enhancing the expression of antioxidant defense genes (Zhang *et al*., 2011) [44]. GA_3 has been tested in saline soils, where foliar applications (100–200 mg L^{-1}) helped maintain cell expansion and shoot growth, resulting in improved cob size and grain set (El-Kamar *et al*., 2013) [14].

2. Hormonal Priming and Yield Parameters

Exogenous SA and BR applications have shown consistent results in improving pollen viability, grain number, and harvest index. In Pakistani field trials, maize plants treated with 1% SA under deficit irrigation had significantly higher grain yield, cob length, and grain protein content compared to untreated controls (Atique-ur-Rehman *et al*., 2019) [5]. Hormonal priming also improved the kernel set under salinity and cold stress through enhanced membrane integrity and hormonal homeostasis (Sultan *et al*., 2021) [32]. In drought-stressed maize, BRs were shown to increase 1000-kernel weight and reduce pollen sterility through regulation of the NO–ABA–BR signaling axis (Trevisan *et al*., 2020) [35].

3. Integration into Crop Management Systems

The integration of growth regulators into maize crop management offers potential for system-level resilience. This includes timing of hormone application, compatibility with fertilizer regimes, and genotype responsiveness. Case studies in India and Pakistan highlight improved crop water productivity and economic yield with MLE (moringa leaf extract) and SA foliar sprays during flowering under water-limited conditions (Waqas *et al*., 2017) [36]. BR and GA_3 have also been integrated into nutrient-stress mitigation protocols, paired with silicon or potassium foliar feeds, showing synergistic effects on grain biomass and mineral content in salt-affected soils (El-Kamar *et al*., 2013) [14].

Table 5: Summary of Field Trials Using Hormone Treatments in Maize

Hormone	Timing	Dose (mg L^{-1})	Target Stage	Outcome	Reference(s)
SA	V6, tasseling	100–300	Drought, salinity	↑ yield, LAI, grain protein, pollen viability	Al Rawi *et al*. (2021) [4]. Atique-ur-Rehman *et al*. (2019) [5].
BR	Pre-anthesis	0.5–1.0	Drought, cold	↑ 1000-grain weight, ↓ sterility, ↑ enzymes	Zhang *et al*. (2011) [44]. Trevisan *et al*. (2020) [35].
GA_3	Vegetative–R1	100–200	Salt stress	↑ cob size, shoot biomass	El-Kamar *et al*. (2013) [14].
SA+MLE	Tasseling–R2	0.5–1.0%	Cold, drought	↑ water productivity, LAI, grain quality	Waqas *et al*. (2017) [36].

Future Prospects and Research Opportunities

The dynamic and intricate role of phytohormones in maize development and stress responses opens new frontiers for integrative research and translational applications. While substantial progress has been made in understanding individual hormone functions, future advances depend on synergizing hormone physiology with modern tools such as phenomics, molecular breeding, and systems biology.

1. Integration of Hormone Physiology with Breeding Pipelines

Incorporating hormonal traits into breeding pipelines can accelerate the development of stress-resilient hybrids. Physiological parameters such as anthesis-silking interval (ASI), pollen viability, hormone ratios (ABA/GA, CK/ABA), and endogenous hormone profiles could serve as selection markers for screening germplasm under stress. Integration of QTL mapping with hormone biosynthesis and signaling genes (e.g., GA20ox, NCED, IPT) can guide marker-assisted selection (MAS) and genomic selection strategies. Hormonal phenotyping tools—including ELISA kits and biosensors—can assist in rapid screening of elite genotypes in field trials.

2. Multi-Hormone Modeling in Field Conditions

Understanding hormone behavior under controlled conditions provides valuable insights, but field conditions present more complex, overlapping stressors. Multi-hormonal models that capture the spatial–temporal fluctuations of hormones and their interactions under real agronomic settings are lacking. Future research should focus on developing crop simulation models incorporating hormonal dynamics, growth stage-specific stress scenarios, and resource availability. Machine learning (ML) and artificial intelligence (AI)-driven models could predict hormonal shifts based on environmental variables, aiding in stress forecasting and input optimization. Field sensors integrated with remote sensing could enable real-time monitoring of hormone-responsive traits like leaf water potential, chlorophyll fluorescence, or canopy temperature.

3. Systems Biology and Omics Approaches

Systems biology offers a promising route for unraveling hormone signaling networks under combined stresses. Integrating transcriptomics, proteomics, metabolomics, and epigenomics can help decipher how hormones regulate and are regulated under multifactorial stress environments. Key transcription factors like DREBs, NACs, and ARFs that coordinate hormonal crosstalk should be mapped across different maize tissues and developmental stages. Co-expression networks and interactome maps can identify hormone hubs and downstream targets relevant for reproductive resilience. CRISPR/Cas9 and synthetic biology could be employed to design hormone-responsive regulatory circuits for precision trait development.

4. Addressing Knowledge Gaps in Hormonal Crosstalk

There is a dearth of research on how multiple hormones interact under dual or sequential stresses such as drought-salinity or heat-nutrient deficiency. The feedback and feedforward loops involving ABA–ET, BR–JA, and GA–CK under these conditions are largely uncharted. Investigating how hormone signaling is modulated by non-hormonal pathways (e.g., ROS, calcium, sugars) will also be essential for constructing comprehensive regulatory models. Field-level validations, especially across diverse agroecological zones, are necessary to translate lab findings into actionable agronomic strategies.

Conclusion

Phytohormones act as central coordinators of maize development and its response to abiotic stress. From seedling vigor and reproductive organ formation to grain filling and maturation, the hormonal network fine-tunes physiological processes in response to environmental cues. This review underscores the importance of individual hormones—such as ABA, auxin, GA, CK, BR, SA, and ethylene—and highlights their synergistic or antagonistic interactions that determine reproductive success and yield stability under stress. Harnessing hormonal knowledge for practical crop improvement requires an interdisciplinary approach. Incorporating hormone profiling into breeding programs, leveraging field-based phenotyping tools, and adopting exogenous hormone treatments during sensitive growth windows can help build resilient maize cropping systems. Ultimately, hormone-based diagnostics, real-time decision support tools, and hormone-informed trait selection strategies hold the promise of enhancing maize productivity in an increasingly volatile climate. Prioritizing these directions will support sustainable intensification and ensure food security across vulnerable agroecosystems.

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