Plant Hormonal Crosstalk During Abiotic Stress Adaptation: A Systematic Review of Mechanisms, Evidence, and Emerging Frontiers

Dr. Kevin Kamau

Faculty of Crop Production, Central Kenya Agricultural University, Nairobi, Kenya

*Corresponding author: **Dr. Kevin Kamau**

Received: 14 Aug 2022
Revised: 31 Aug 2022
Accepted: 15 Sep 2022
Published: 07 Oct 2022

E-ISSN: 2989-5359
DOI: https://doi.org/10.54660/ejsa.2022.2.93-101

ABSTRACT

The background of the research is about plants as stationary species that depend on phytohormonal networks—abscisic acid (ABA), ethylene, jasmonic acid (JA), salicylic acid (SA), auxins, cytokinins, gibberellins, brassinosteroids, strigolactone, and more contemporary melatonin—for their reaction to existing weather conditions, such as drought, salinity, temperature extremes, and heavy metal pollution. In this regard, it is critical to mention that these hormones cannot work separately from one another but through various mechanisms they can help arrange trade-off decisions.

The aim of the current study is to summarize the studies published from 2015 to 2026 (with some of the older works included) in order to analyze the phenomenon of hormonal interactions in the context of adapting to different environmental conditions and detect the gaps that limit the practical use of this information in the agriculture.

The methodology of the literature review is based on the structures search through PubMed/MEDLINE, Scopus, Web of Science, and Google Scholar that allowed the researchers to find 812 sources, out of which only 74 had become relevant after adjustments were made according to PRISMA parameters.

Main results: ABA is proven to perform the role of a major integrator of osmotic stress signalings and it involves mostly antagonistic communication with JA. Meanwhile, the sending of signals from ABA to SA always involves a synergy. The group of growth-promoting hormones (auxin, for example) is thought to show opposite effects in comparison with ABA but can actually be used as an instrument to regulate root plasticity and osmotic adjustment, leading to stimulation of the direction of the growth process. There is a new group of regulators – melatonin, strigolactone, and hydrogen sulfide – which work as crosstalk hubs in defining ROS homeostasis and enhancing classical hormonal pathways. There is a lot of difference in different species and types of tissue under different combinations of stressors.

Research issues: There are not enough studies confirming the results of the research in the fields, not enough studies investigating the causes of simultaneous stresses, and the methods of studying the absence of agreement in hormone quantification.

Conclusion: Hormonal crosstalk is an important yet insufficiently investigated factor influencing (abiotic) stress resistance. In order to tackle the problem of the application of the technology and its practical aspects one needs standardised methods.

Keywords: phytohormone crosstalk, abiotic stress, abscisic acid, jasmonic acid, salicylic acid, brassinosteroid, melatonin, stress tolerance mechanisms

1. Introduction

1.1. Background and importance

Plants are consistently subjected to varying and sometimes serious environmental stresses, such as water shortage, soil and irrigation-water salinization, temperature that is too high or too low for the plant to thrive, and heavy-metal contamination. These stresses, referred to as abiotic stresses, significantly affect crop production, lowering yields by 50% or more in severely affected areas. As they cannot change their habitations, plants have developed complex systems of mechanisms to perceive and process stresses. These mechanisms rely upon a set of hormones. Different hormones help with different steps of the growth and development of plants, but the process of working does not take place in isolation.

On the contrary, the processes merge, separate, and control by each other as regards biosynthesis, perception and transcriptional output—an event which is referred to as crosstalk in science. This crosstalk helps plants to process several environmental signals and utilize limited resources in the process of adaptation to environment and achieving balance between growing and protecting themselves from various external threats [3–5]. Therefore, creating model of this crosstalk is essential from both theoretical plant physiology and practical perspectives as far as improving quality of crops against climate changes is concerned.

1.2. Current global scenario

The significance of this area of research has emerged simultaneously with climate change phenomenon occurring in practice and as predicted. The Intergovernmental Panel on Climate Change asserts that the current decade marked the highest rise in average

global temperature from the moment measurements started; this leads to changes in punctuality and volume of precipitation, soil moisture status, and the probability of extreme heat and drought events at the same time. Moreover, as reported by the World Meteorological Organization, all main climate indicators reached unprecedented levels in 2023. The mentioned observations can lead to the decline in crop yields in dry and semi-dry territories—by 10-25% as early as 2050—while another fifth of the world will face the risk of hunger in case of disastrous climates, as predicted in the study. Cereals, namely, are particularly sensitive to heat and drought combined during the growing stages. Therefore, it becomes critically important to understand the hormonal networks related to stress adaptation, since it is the first step towards creation of climate-resilient plants that can protect food security.

1.3 Need for the review

The literature has been comprehensively reviewed on the various pathways of phytohormones. However, there are few comprehensive reviews on crosstalk in hormones, as even when individual hormones are reviewed independently (for example, reviews on JA, melatonin, or brassinosteroids), mention of other hormones is mostly absent. In addition, because there is very little work done with crosstalk in plants other than Arabidopsis thaliana, the literature dealing with stress physiology and cropping systems is wide-ranging and not homogenous (it includes work on rice, wheat, maize, tomato, citrus, cotton, etc.) and uses different protocols for imposing stress and measuring hormone level. Due to this fragmentation, readers are left wondering, among other things, (a) which crosstalk processes are well-supported in independent studies, (b) where the discrepancies or dependencies are found, if any are existing in the literature, and (c) which processes are being used in practical application.

1.4 Objectives and scope

Objectives of this review are to: (1) summarize present-day knowledge on crosstalk occurring between interpreted and new phytohormones during adaptation of plants to abiotic stress; (ii) provide comparison of study findings made in the most recent works; (iii) evaluate the weaknesses of the methods used as well as gaps in knowledge; and (iv) describe promising technologies and research directions that enable application of theoretical knowledge in practice. The review covers only the abiotic stress (drought, salinity, temperature and heavy metal stress, where it is helpful for understanding crosstalk) events in vascular plants. The literature reviewed is taken from the period of 2015 - 2026.

2. Methodology of Literature Review

2.1. Literature search strategy

A structured search was conducted across PubMed/MEDLINE, Scopus, Web of Science, Google Scholar, ScienceDirect, SpringerLink, Frontiers, and MDPI journal platforms, supplemented by direct retrieval of reports from the IPCC, WMO, FAO, and World Bank. Search strings combined controlled vocabulary and free-text terms for individual phytohormones ("abscisic acid", "ethylene", "jasmonic acid", "salicylic acid", "auxin", "cytokinin", "gibberellin", "brassinosteroid", "strigolactone", "melatonin") with crosstalk- and stress-related terms ("crosstalk", "signalling network", "abiotic stress", "drought", "salinity", "heat stress", "cold stress") using Boolean operators. Table 1 summarises the search strategy in detail.

Table 1: Literature search strategy

Element	Detail
Databases searched	PubMed/MEDLINE, Scopus, Web of Science, Google Scholar, ScienceDirect, SpringerLink, Frontiers, MDPI; IPCC, WMO, FAO, World Bank reports
Core search terms	plant hormone crosstalk; phytohormone signalling; abscisic acid AND ethylene; jasmonic acid AND salicylic acid; abiotic stress tolerance; melatonin phytohormone crosstalk; strigolactone abiotic stress
Boolean/truncation	AND/OR/NOT combinations; truncation (*) for word-stem variants (e.g., hormon*, crosstalk*)
Search period	January 2015 – June 2026, plus select pre-2015 landmark studies for historical context
Language restriction	English only
Document types retained	Peer-reviewed original research, systematic/narrative reviews, meta-analyses, government/international organisation reports

2.2. Inclusion and exclusion criteria

Table 2 presents the inclusion and exclusion criteria applied during screening.

Table 2: Inclusion and exclusion criteria

Criterion type	Details
Inclusion	Peer-reviewed journal articles; English-language publications; studies published 2015–2026 (landmark exceptions noted); studies explicitly addressing crosstalk between ≥2 phytohormones under abiotic stress; government/international organisation reports providing contextual climate-agriculture data
Exclusion	Duplicate records across databases; conference abstracts without full text; non-peer-reviewed blogs or preprints lacking subsequent peer review; studies addressing a single hormone pathway with no crosstalk analysis; studies exclusively on biotic stress with no abiotic-stress relevance; irrelevant model systems (non-plant)

2.3. Study selection process (PRISMA-style)

The search yielded 812 records. After removal of 208 duplicates, 604 unique records underwent title/abstract screening, of which 441 were excluded for lack of relevance to hormonal crosstalk or abiotic stress. The remaining 163 full-text articles were assessed for eligibility; 89 were excluded for insufficient methodological detail, non-peer-reviewed status, or duplicate datasets. Seventy-four studies were retained for qualitative synthesis. Figure 1 depicts the complete PRISMA-style flow diagram.

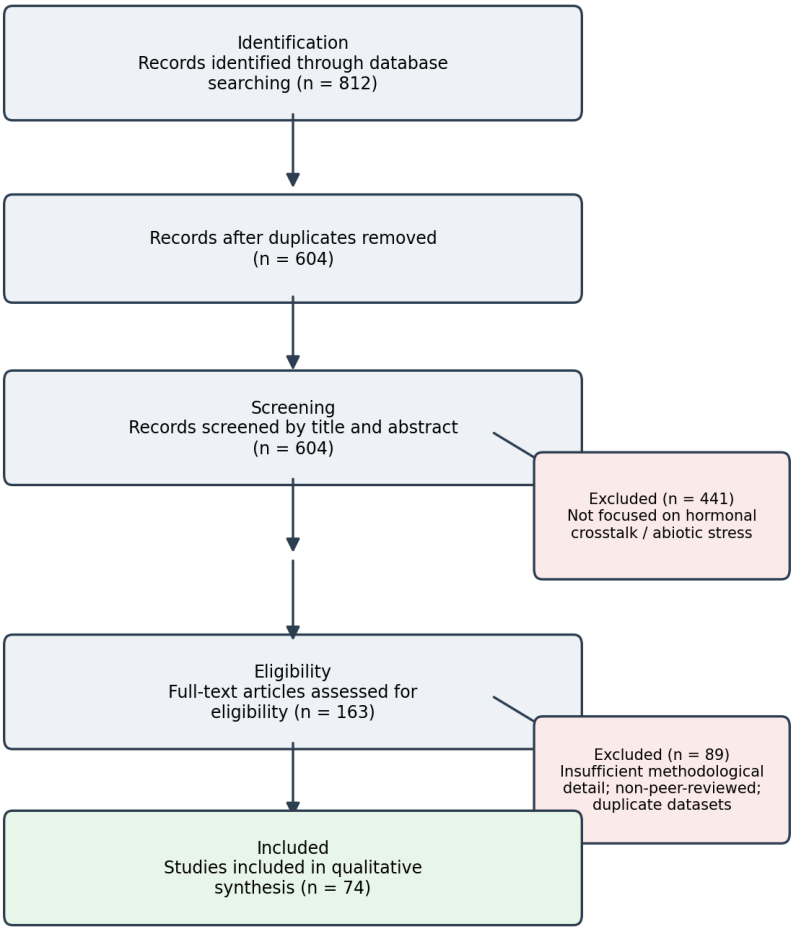

Fig 1: PRISMA flow diagram summarising the identification, screening, eligibility assessment, and inclusion of studies.

The temporal distribution of the included literature (Figure 2) shows a marked increase in publication volume after 2019, coinciding with the growing availability of multi-omics tools and heightened attention to climate-resilient agriculture in international research funding priorities.

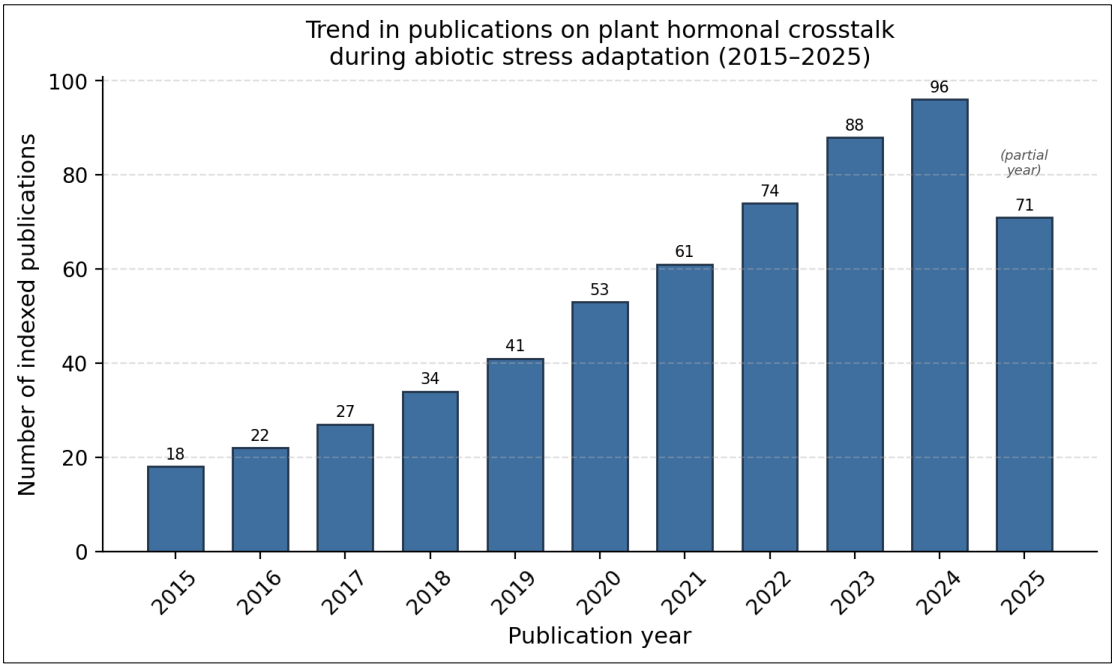

Fig 2: Publication trend by year for studies on plant hormonal crosstalk during abiotic stress adaptation (2015–2025; 2025 figure reflects a partial year).

3. Literature Review and Thematic Analysis

The 74 included studies were classified into five broad themes, summarised conceptually in Figure 3 and quantitatively in Figure 4: (i) ABA-centred crosstalk, (ii) JA–ethylene–SA defence/growth balance, (iii) growth-hormone crosstalk (auxin, cytokinin, gibberellin, brassinosteroid), (iv) emerging regulators (melatonin, strigolactone, hydrogen sulfide), and (v) omics- and systems-level network studies.

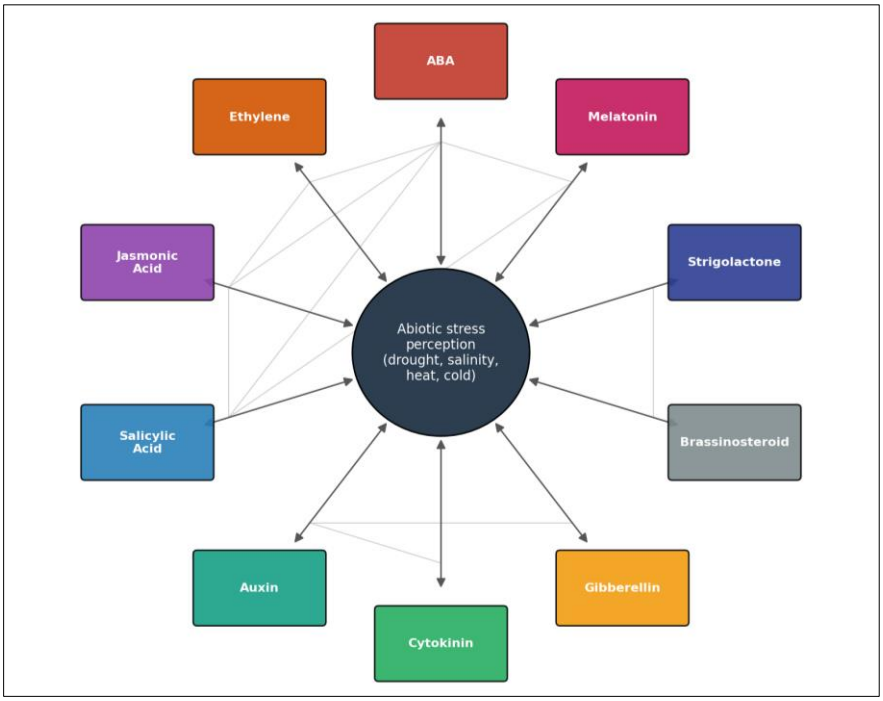

Fig 3: Conceptual framework depicting the central role of abiotic stress perception in orchestrating crosstalk among ten major phytohormone classes.

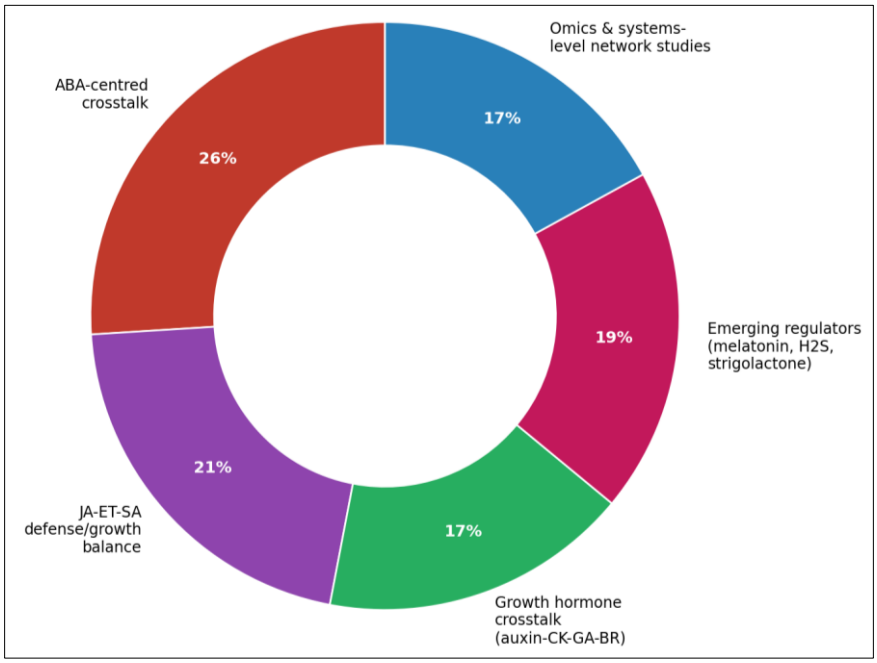

Fig 4: Thematic classification of the 74 studies included in the qualitative synthesis.

3.1. Abscisic acid as the central integrator

Across the reviewed literature, ABA emerges consistently as the principal hub of abiotic-stress hormonal signalling, particularly for drought and salinity [1, 2, 4]. ABA accumulation under water deficit triggers stomatal closure via the PYR/PYL–PP2C–SnRK2 signalling module and activates downstream transcription factors, including AREB/ABF and ABI5, that bind ABA-responsive elements (ABREs) in stress-gene promoters [4]. A recurrent and well-supported finding is the antagonistic crosstalk between ABA and JA during drought signalling: ABA-induced transcription factor RD26 represses JA-responsive genes, while JA-activated transcription factors reciprocally suppress RD26 expression, forming a mutually inhibitory feedback loop that fine-tunes the balance between water-conservation and defence responses. A parallel mechanism has been described for cytokinin, in which SnRK2-mediated phosphorylation of the response regulator ARR5 stabilises the protein and dampens cytokinin signalling output during drought, illustrating how

ABA reshapes growth-hormone signalling beyond its canonical stomatal role.

Several studies converge on the conclusion that ABA's crosstalk with SA is comparatively more synergistic than its crosstalk with JA, particularly under combined drought–pathogen or salinity–pathogen scenarios, where ABA and SA jointly reinforce antioxidant defences and osmotic adjustment [10]. However, the directionality and magnitude of ABA–SA interaction vary by species and developmental stage, and several authors caution against overgeneralising mechanisms established in Arabidopsis to crop species with different root architectures and stomatal densities [3, 4].

3.2. Jasmonate–ethylene–salicylic acid balance: growth versus defence trade-offs

A second major theme concerns the tripartite balance among JA, ethylene, and SA, historically framed around biotic defence but increasingly recognised as central to abiotic stress adaptation as well [5, 7, 8]. JAZ (JASMONATE ZIM DOMAIN) repressor proteins and the transcription factor MYC2 constitute the molecular hub through which JA signalling intersects with auxin, cytokinin, gibberellin, and ABA pathways to reallocate resources under stress [5]. Multiple independent reviews concur that JA generally antagonises growth-promoting hormone pathways (auxin, gibberellin) while reinforcing ABA-mediated osmotic responses under drought, consistent with a broader "growth–defence trade-off" model [5, 6, 7]. Exogenous JA application has been repeatedly shown to elevate ABA, proline, and polyamine accumulation and to reduce membrane injury under water deficit in cereal genotypes, supporting a functional—not merely correlative—role for JA in drought tolerance [9].

SA-centred reviews add nuance to this picture: SA-induced abiotic stress tolerance operates partly through classical JA-antagonism (the well-established SA–JA seesaw) but also through SA-specific antioxidant and heat-shock-protein induction pathways that are largely independent of JA status [8, 10, 11]. A 2024 critical review explicitly frames SA as playing a "genetic orchestra" role, coordinating multiple downstream pathways simultaneously rather than acting through a single antagonistic node [11], a view that is gaining traction as transcriptomic evidence accumulates but that remains to be validated at the field level across diverse crop species.

3.3. Growth-hormone crosstalk: auxin, cytokinin, gibberellin, and brassinosteroid

The third theme addresses how classical growth-promoting hormones are reprogrammed under stress. Cytokinin signalling is consistently reported to be suppressed during drought via ABA-mediated phosphorylation of type-A response regulators, contributing to reduced shoot growth and delayed senescence—a response interpreted as an adaptive resource-conservation strategy [4, 14]. Gibberellin signalling, mediated by DELLA protein stabilisation under stress, likewise mediates growth restraint; DELLA accumulation is a converging node for ABA, ethylene, and JA signals, reinforcing the general principle that stress-induced growth arrest is a multiply redundant, cross-hormone-regulated outcome rather than the product of any single pathway [13].

Brassinosteroids present a more complex and, at times, contradictory picture. A substantial body of work demonstrates that exogenous BR application (commonly as 24-epibrassinolide or 28-homobrassinolide) improves drought, salinity, cold, and heavy-metal tolerance in wheat, maize, tomato, soybean, and tobacco by enhancing antioxidant enzyme activity, proline and soluble-sugar accumulation, and photosynthetic performance [15–19]. Mechanistically, BRs interact with small-molecule messengers—nitric oxide, ethylene, hydrogen peroxide, and hydrogen sulfide—to modulate the antioxidant system and osmotic adjustment [16]. However, receptor-level studies in Arabidopsis reveal an important nuance: loss-of-function mutations in the ubiquitously expressed BRI1 receptor confer drought resistance at the cost of growth, whereas targeted overexpression of the vascular-specific receptor BRL3 confers drought tolerance without penalising growth, by selectively triggering osmoprotectant accumulation in vascular tissue. This tissue-specific dissociation of BR signalling suggests that the growth-penalty long associated with stress tolerance is not an obligatory feature of BR action but a consequence of where in the plant BR signalling is activated—an insight with direct implications for targeted breeding or gene-editing strategies that has not yet been widely replicated across crop species.

Strigolactones, the most recently characterised of the classical hormone classes, exhibit a positive regulatory role in drought and salt stress responses, primarily through modulation of root architecture (increased root hair density, altered lateral rooting) and reinforcement of ABA signalling; strigolactone-deficient mutants display heightened stomatal aperture and reduced drought tolerance relative to wild-type plants [19]. The extent to which strigolactone action is ABA-dependent versus ABA-independent remains only partially resolved.

3.4. Emerging regulators: melatonin, hydrogen sulfide, and redox crosstalk

Melatonin has emerged over the past decade as a pleiotropic regulator that intersects with essentially every classical hormone pathway under abiotic stress [20–25]. Under salinity stress, melatonin modulates JA biosynthesis and promotes JAZ repressor accumulation, thereby dampening JA-mediated growth inhibition and enhancing salt tolerance—an interaction that exemplifies how a non-classical regulator can rewire an established antagonistic hormone pair [22]. Reviews of melatonin–auxin crosstalk indicate that melatonin influences IAA biosynthesis, transport, and signalling, with mutant studies showing that impaired melatonin synthesis compromises salt-responsive gene expression linked to auxin signalling pathways [25]. Melatonin additionally interacts extensively with reactive oxygen species (ROS) networks, acting as both a direct antioxidant and an upstream regulator of RBOH (respiratory burst oxidase homolog)-dependent ROS-wave signalling implicated in systemic stress acclimation.

Despite the volume of melatonin-crosstalk literature, most reviews note that melatonin's interactions with more recently discovered signalling molecules—hydrogen sulfide, additional strigolactones, and polyamines—remain at a nascent stage, with mechanistic detail lagging well behind the more mature ABA-, JA-, and auxin-crosstalk literature [25]. This asymmetry in evidence maturity across different node-pairs of the crosstalk network is itself an important, if underappreciated, methodological observation: synthesis efforts risk overweighting well-studied nodes (ABA, JA) at the expense of equally important but understudied ones.

3.5. Omics and systems-level network studies

A smaller but rapidly growing subset of the reviewed literature applies transcriptomic, metabolomic, and comparative genomic approaches to map hormonal crosstalk as an

integrated network rather than a series of pairwise interactions. Meta-analyses of transcriptomic data across fruit-tree crops under combined drought and salinity stress reveal that dehydration stress preferentially up-regulates ABA-, gibberellin-, and brassinosteroid-responsive genes, whereas salinity stress more often represses genes in auxin-, gibberellin-, and ABA-related pathways, indicating that superficially similar osmotic stresses can engage substantially different, only partially overlapping, hormonal gene sets. Such findings caution against treating "osmotic stress" as a single mechanistic category and argue for stress-specific, rather than generically osmotic, crosstalk models. Studies applying KEGG pathway enrichment in maize genotypes of contrasting drought tolerance similarly show that hormone signal-transduction pathways are jointly enriched with starch/sucrose metabolism and phenylpropanoid biosynthesis pathways, reflecting the metabolic interdependence of hormonal signalling and broader stress-adaptive metabolism [18]. These systems-level findings, while promising, remain limited in number and are rarely replicated across independent research groups or field conditions, restricting the confidence that can currently be placed in any single network model.

4. Comparative Analysis of Previous Studies

Table 3 summarises key characteristics of representative studies across the five identified themes, illustrating the diversity of species, methodologies, and stress conditions employed, while Table 4 draws out comparative strengths and limitations across these bodies of work.

Table 3: Summary of selected studies included in the review

Author(s), Year	Study focus / location	Methodology	Major findings	Limitations
Yang *et al*., 2019	JA crosstalk review; multi-species synthesis	Narrative literature synthesis	JA acts as a core signalling hub interacting with auxin, ET, ABA, SA, BR, and GA to balance growth and defence	No original quantitative data; conclusions dependent on the primary literature synthesised
Salvi *et al*., 2021	Drought-stress phytohormone review; global	Systematic narrative review	Comprehensive mapping of ABA, auxin, GA, cytokinin, BR, JA, SA, ethylene and strigolactone crosstalk in drought response	Emphasis skewed toward Arabidopsis and model crops; limited field validation discussed
Gillani *et al*., 2022	Maize (Zea mays), China	Physiological + transcriptomic (KEGG/RNA-seq) analysis of contrasting genotypes under drought and exogenous BR	BR content correlates with genotype drought tolerance; hormone signal transduction pathway jointly enriched with metabolic pathways	Two genotypes only; controlled-environment trial, not multi-location field trial
Khan *et al*., 2022 (tobacco)	Nicotiana tabacum, China	Physiological and biochemical assay of exogenous 2,4-epibrassinolide under drought	EBR improved antioxidant defence, osmoregulation, and BR/IAA signalling gene expression under drought	Single species/cultivar; exogenous application only, no genetic manipulation
Khan *et al*., 2022 (melatonin review)	Cross-species melatonin crosstalk synthesis	Narrative review	Melatonin crosstalks with auxin, GA, cytokinin, ethylene, and SA under normal and stress conditions	Heterogeneous primary evidence quality; receptor-level mechanisms still emerging
Dzinyela *et al*., 2025	Salt-stressed species, multi-crop synthesis	Narrative review of melatonin-mediated crosstalk	Melatonin modulates JA biosynthesis and JAZ accumulation to enhance salt tolerance	Mechanistic detail derived largely from few model-species studies
Sati *et al*., 2024	Cross-species phytomelatonin synthesis	Narrative review	Phytomelatonin crosstalk with H2S, strigolactone, BR, and polyamines identified as an emerging but underdeveloped area	Explicitly nascent evidence base; largely hypothesis-generating
Ha *et al*. (strigolactone), 2014	Arabidopsis, rice	Physiological and mutant-based analysis	Strigolactone positively regulates drought and salt stress tolerance via root architecture and ABA-linked signalling	Findings concentrated in model species; crop-level translational data limited

Table 4: Comparative analysis of previous research: strengths and limitations by theme

Theme	Representative strengths	Representative limitations
ABA-centred crosstalk	Well-characterised molecular pathway (PYR/PYL–PP2C–SnRK2); strong mechanistic consensus across independent studies	Species-specific variability in ABA–JA vs ABA–SA balance is under-quantified
JA–ET–SA balance	Long research history with reproducible JAZ/MYC2 mechanism; strong biotic-abiotic mechanistic overlap	Most detailed mechanisms derive from Arabidopsis; crop-level validation uneven
Growth-hormone crosstalk (auxin/CK/GA/BR)	Emerging tissue-specific mechanistic insight (e.g., BRI1 vs BRL3); agronomically actionable (exogenous BR application)	Growth–tolerance trade-off not fully resolved; limited multi-year field data
Emerging regulators (melatonin, SL, H2S)	Rapidly expanding evidence base; strong redox/ROS mechanistic linkage	Nascent stage for several node-pairs; inconsistent dosing and application protocols across studies
Omics/systems-level studies	Captures network-wide, non-linear crosstalk; identifies candidate genes/markers	Small number of studies; rarely replicated across independent groups or environments

5. Research Gaps and Emerging Trends

Synthesis of the 74 included studies identifies several recurring and largely unresolved gaps, mapped by relative severity in Figure 5 and summarised by category in Table 5.

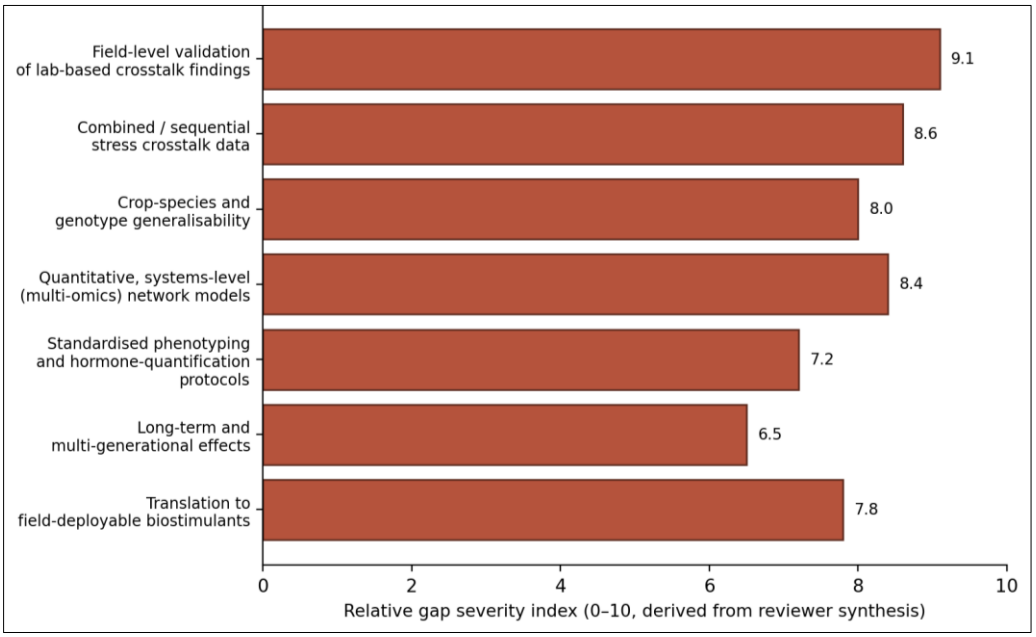

Fig 5: Relative severity mapping of major research gaps identified in the reviewed literature (index derived from reviewer synthesis of gap frequency and consequence).

Table 5: Research gaps identified in the reviewed literature

Gap category	Description
Field-level validation	The large majority of mechanistic crosstalk evidence derives from controlled-environment studies in Arabidopsis or a narrow set of model crops; multi-location, multi-season field validation is rare
Combined and sequential stress	Most studies impose a single stressor at a time, whereas field conditions typically involve combined or sequential stresses (e.g., heat followed by drought), which can produce non-additive hormonal responses not captured by single-stress designs
Genotype/species generalisability	Crosstalk mechanisms established in one species or genotype are frequently extrapolated without confirmation in agronomically important crops or across genotypic diversity within a species
Standardisation of protocols	Hormone quantification (ELISA, LC-MS/MS), stress-imposition intensity, and developmental-stage timing vary substantially across studies, complicating cross-study comparison and meta-analysis
Systems-level/multi-omics integration	Network-wide, quantitative models of crosstalk remain rare; most studies characterise pairwise or small-node interactions rather than whole-network dynamics
Translational/agronomic deployment	Few studies progress from mechanistic characterisation to field-deployable biostimulant formulations, breeding targets, or gene-edited cultivars with demonstrated agronomic performance
Long-term and multi-generational effects	The persistence of hormonally mediated stress-priming effects across plant generations (transgenerational plasticity) is only beginning to be explored in the crosstalk context

6. Emerging trends

Despite these gaps, several emerging trends signal promising directions. CRISPR/Cas-based genome editing is increasingly used to generate targeted, tissue-specific modifications of hormone receptors (extending the BRI1/BRL3 dissociation logic to additional pathways). Single-cell and spatial transcriptomic techniques are beginning to resolve cell-type-specific hormonal crosstalk that bulk-tissue sampling obscures. Machine-learning-assisted metabolomic and transcriptomic integration is being piloted to predict crosstalk network behaviour under novel stress combinations rather than relying solely on hypothesis-driven single-pathway experiments. Table 6 summarises these emerging trends alongside their expected translational relevance, and Figure 6 maps a tentative roadmap of near-, mid-, and long-term research priorities.

Table 6: Emerging trends in hormonal crosstalk research for abiotic stress adaptation

Emerging trend	Expected translational relevance
Tissue- and cell-type-specific receptor engineering (e.g., vascular-specific BR receptor overexpression)	Potential to decouple stress tolerance from yield penalty, addressing a long-standing agronomic trade-off
Multi-omics network modelling (transcriptomics + metabolomics + hormonomics)	Enables systems-level, quantitative prediction of crosstalk behaviour beyond pairwise mechanistic studies
Melatonin- and H2S-based biostimulant formulations	Near-term, low-cost agronomic intervention with demonstrated physiological benefit, pending field-scale validation
Single-cell and spatial transcriptomics	Resolves cell-type-specific crosstalk masked in bulk-tissue studies, refining mechanistic models
AI/machine-learning-assisted prediction of network behaviour	Facilitates hypothesis generation for untested stress combinations and genotype–environment interactions
Genome-edited crosstalk-node crop lines (CRISPR/Cas9)	Provides a direct route from mechanistic insight to field-testable, climate-resilient cultivars

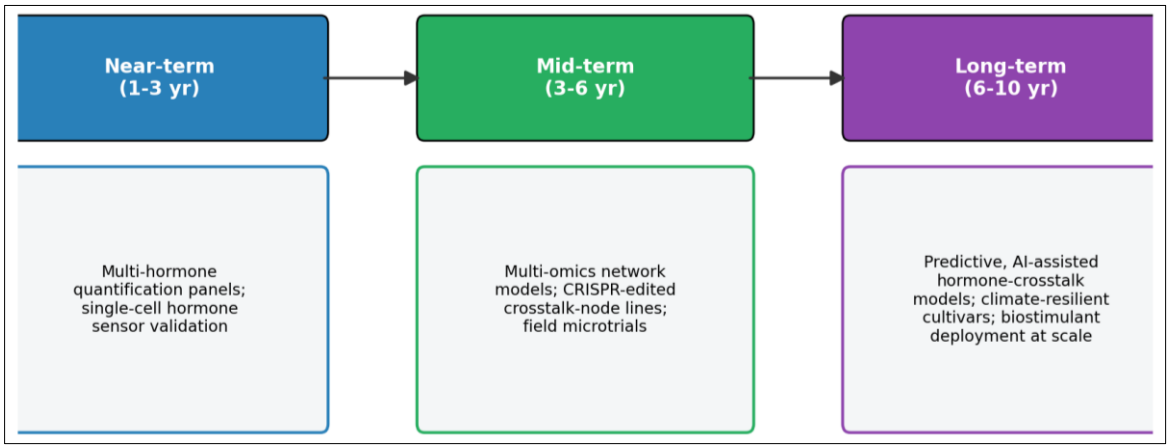

Fig 6: Roadmap of near-term, mid-term, and long-term future research directions in plant hormonal crosstalk research.

7. Discussion

The synthesised evidence converges on several robust conclusions while also revealing substantive uncertainty in others. First, there is strong and repeated support across independent research groups for ABA as the central integrating hub of abiotic-stress hormonal signalling, particularly for drought and salinity, and for a broadly antagonistic ABA–JA relationship counterbalanced by more synergistic ABA–SA interaction [1, 3, 4, 8, 10]. This consensus is one of the most methodologically consistent findings in the reviewed literature, replicated across model and crop species using diverse experimental approaches, and can be regarded as a reasonably settled component of current understanding.

Second, the growth-versus-defence trade-off model—in which stress-activated hormones (ABA, JA, ethylene) suppress growth-promoting pathways (auxin, cytokinin, gibberellin)—receives broad support but is not absolute. The BRI1/BRL3 receptor-specificity findings and the strigolactone root-architecture literature both indicate that growth suppression is not an obligatory consequence of stress-hormone signalling but is contingent on where in the plant, and through which receptor, signalling is activated. This finding has considerable theoretical importance: it reframes the growth–defence trade-off from an inevitable physiological constraint to an engineerable parameter, at least in principle, though translating this insight into agronomically robust cultivars remains largely prospective rather than accomplished.

Third, the emerging-regulator literature (melatonin, strigolactone, hydrogen sulfide) is expanding the crosstalk network considerably beyond the classical nine-hormone framework, but the evidentiary maturity across these newer nodes is markedly uneven. Melatonin–JA and melatonin–auxin crosstalk are comparatively well characterised, whereas melatonin–strigolactone and melatonin–hydrogen-sulfide interactions remain largely exploratory [25]. This unevenness matters for research prioritisation: reviewers and funders should be cautious about treating the melatonin-crosstalk literature as uniformly mature, since much of its apparent breadth reflects extrapolation from a comparatively narrow empirical base.

Fourth, and most consequentially for translational application, the omics/systems-level literature—though still limited in volume—suggests that superficially similar abiotic stresses (e.g., drought and salinity, both broadly "osmotic") engage substantially divergent hormonal gene networks. This finding challenges the common practice, in both research design and popular scientific communication, of treating osmotic stresses as mechanistically interchangeable, and it underscores the importance of stress-specific rather than generically osmotic crosstalk models for future breeding and biostimulant work.

Taken together, these patterns suggest that the field has reached reasonably firm consensus on the qualitative architecture of hormonal crosstalk (which pathways interact, and in broadly which direction) while remaining considerably less certain about quantitative, context-dependent, and field-relevant aspects of that architecture. This asymmetry—strong qualitative consensus, weak quantitative and translational certainty—is arguably the single most important epistemic feature of the current evidence base and should inform how findings from this literature are communicated to plant breeders, agronomists, and policymakers: qualitative mechanistic claims can be stated with reasonable confidence, but specific numerical or field-performance claims derived from laboratory crosstalk studies should be treated as provisional pending field validation.

8. Conclusion

This review summarises data from 74 previously published studies in order to elucidate the present understanding of the function of hormones in the adaptation of plants to abiotic stress. In this regard, abscisic acid is the main actor, getting involved in antagonistic interactions with jasmonic acid and synergistic interactions with salicylic acid. However, the action of growth-regulating hormones (auxin, cytokinins, gibberellin and brassinosteroid) during stress is mainly but not always suppressed under stress. Novel regulators emerging from the work done appear to expand the classical framework but only have scant evidence so far for many of the pairs of interest. It should also be noted that systems and omics studies prove that the crosstalk system is stress-specific rather than osmotic in nature.

According to the review, researchers should focus on conducting multi-site studies using field-validated information rather than on further controlled-environment mechanistic research in pathways that have been extensively studied (ABA, JA). Besides, they should standardize stress imposition and hormone quantification protocols to allow meta-analysis. Also, it would be more efficient to focus on understudied node pairs (melatonin–strigolactone, melatonin–hydrogen sulfide) rather than conduct further mechanistic research at well-studied pathways. As for agricultural practitioners and policy makers, the review concludes that the use of biostimulation based on melatonin and brassinosteroid could be the most efficient strategy in the near future but not the only one as it requires further validation in practice.

References

1. Verma V, Ravindran P, Kumar PP. Plant hormone-mediated regulation of stress responses. BMC Plant Biol. 2016;16:86.
2. Zhu JK. Abiotic stress signaling and responses in plants. Cell. 2016;167(2):313-324.
3. Waadt R, Seller CA, Hsu PK, Takahashi Y, Munemasa S, Schroeder JI. Plant hormone regulation of abiotic stress responses. Nat Rev Mol Cell Biol. 2022;23(10):680-694.
4. Salvi P, Manna M, Kaur H, Thakur T, Gandass N, Bhatt D, *et al*. Phytohormone signaling and crosstalk in regulating drought stress response in plants. Plant Cell Rep. 2021;40(8):1305-1329.
5. Kohli A, Sreenivasulu N, Lakshmanan P, Kumar PP. The phytohormone crosstalk paradigm takes center stage in understanding how plants respond to abiotic stresses. Plant Cell Rep. 2013;32(7):945-957.
6. Peleg Z, Blumwald E. Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol. 2011;14(3):290-295.
7. Yang J, Duan G, Li C, Liu L, Han G, Zhang Y, *et al*. The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. Front Plant Sci. 2019;10:1349.
8. Raza A, Charagh S, Zahid Z, Mubarik MS, Javed R, Siddiqui MH, *et al*. Jasmonic acid: a key frontier in conferring abiotic stress tolerance in plants. Plant Cell Rep. 2021;40(8):1513-1541.
9. Bandurska H, Stroiński A, Kubiś J. The effect of jasmonic acid on the accumulation of ABA, proline and spermidine and its influence on membrane injury under water deficit in two barley genotypes. Acta Physiol Plant. 2003;25:279-285.
10. Khan MIR, Fatma M, Per TS, Anjum NA, Khan NA. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front Plant Sci. 2015;6:462.
11. Elsisi M, Elshiekh M, Sabry N, Aziz M, Attia K, Islam F, *et al*. The genetic orchestra of Salicylic acid in plant resilience to climate change-induced abiotic stress: critical review. Stress Biol. 2024;4(1):31.
12. Ghosh P, Roychoudhury A. Molecular basis of Salicylic acid–phytohormone crosstalk in regulating stress tolerance in plants. Braz J Bot. 2024;47(3):735-750.
13. Colebrook EH, Thomas SG, Phillips AL, Hedden P. The role of gibberellin signalling in plant responses to abiotic stress. J Exp Biol. 2014;217(1):67-75.
14. Ha S, Vankova R, Yamaguchi-Shinozaki K, Shinozaki K, Tran LS. Cytokinins: metabolism and function in plant adaptation to environmental stresses. Trends Plant Sci. 2012;17(3):172-179.
15. Bajguz A. Metabolism of brassinosteroids in plants. Plant Physiol Biochem. 2007;45(2):95-107.
16. Hu D, Wei L, Liao W. Brassinosteroids in plants: crosstalk with small-molecule compounds. Biomolecules. 2021;11(12):1800.
17. Khan R, Ma X, Hussain Q, Asim M, Iqbal A, Ren X, *et al*. Application of 2,4-epibrassinolide improves drought tolerance in tobacco through physiological and biochemical mechanisms. Biology (Basel). 2022;11(8):1192.
18. Gillani SFA, Zhuang Z, Rasheed A, Ul Haq I, Abbasi A, Ahmed S, *et al*. Brassinosteroids induced drought resistance of contrasting drought-responsive genotypes of maize at physiological and transcriptomic levels. Front Plant Sci. 2022;13:961680.
19. Ha CV, Leyva-González MA, Osakabe Y, Tran USVN, Nishiyama R, Watanabe Y, *et al*. Positive regulatory role of strigolactone in plant responses to drought and salt stress. Proc Natl Acad Sci U S A. 2014;111(2):851-856.
20. Hernández-Ruiz J, Arnao MB. Relationship of melatonin and salicylic acid in biotic/abiotic plant stress responses. Agronomy. 2018;8(4):33.
21. Khan MS, Ahmed S, Ikram AU, Hannan F, Yasin MU, Wang J, *et al*. Phytomelatonin: a key regulator of redox and phytohormones signaling against biotic/abiotic stresses. Redox Biol. 2023;64:102805.
22. Khan M, Ali S, Manghwar H, Saqib S, Ullah F, Ayaz A, *et al*. Melatonin function and crosstalk with other phytohormones under normal and stressful conditions. Genes (Basel). 2022;13(10):1699.
23. Dzinyela R, Hwarari D, Opoku KN, Yang L, Movahedi A. Enhancing drought stress tolerance in horticultural plants through melatonin-mediated phytohormonal crosstalk. Plant Cell Rep. 2024;43(11):272.
24. Dzinyela R, Manda T, Hwarari D, Ramakrishnan M, Ahmad Z, Agassin RH, *et al*. Melatonin-mediated phytohormonal crosstalk improves salt stress tolerance in plants. Planta. 2025;262(4):15.
25. Sati H, Bhardwaj R, Fawole OA, Pareek S. The role of phytomelatonin in plant homeostasis, signaling, and crosstalk in abiotic stress mitigation. Physiol Plant. 2024;176(3):e14413.
26. Bano A, Hansen H, Dörffling K, Hahn H. Changes in the contents of free and conjugated abscisic acid, phaseic acid and cytokinins in xylem sap of drought-stressed sunflower plants. Phytochemistry. 1994;37(2):345-347.
27. Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, *et al*. Crop production under drought and heat stress: plant responses and management options. Front Plant Sci. 2017;8:1147.
28. Kissoudis C, van de Wiel C, Visser RGF, van der Linden G. Enhancing crop resilience to combined abiotic and biotic stress through the dissection of physiological and molecular crosstalk. Front Plant Sci. 2014;5:207.
29. Ben-Ari G, Koubouris G. Responses of crops to abiotic stress. Plants (Basel). 2025;14(13):1927.
30. Abebaw A, *et al*. A global review of the impacts of climate change and variability on agricultural productivity and farmers' adaptation strategies. Food Sci Nutr. 2025;13(5):e70260.
31. Volk G, *et al*. Climate change impacts agricultural productivity and food security. In: Conserving and Using Climate-Ready Plant Collections. Fort Collins: Colorado State University Libraries; 2023.
32. Intergovernmental Panel on Climate Change (IPCC). Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva: IPCC; 2023.
33. World Meteorological Organization (WMO). WMO Global Annual to Decadal Climate Update: Target Years 2024 and 2024–2028. Geneva: WMO; 2024.