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REVIEW PAPER

Interplay between auxin and abiotic stresses in maize

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Abstract

Plants display a continuum of responses to abiotic stresses, including sensitivity and tolerance. Classical phytohormones have been implicated in these processes due to the observed changes in growth phenotypes following stress cues. This interplay is often described as the growth–stress trade-off. Recent studies have examined abiotic stress responses in maize and implicated auxin biosynthesis, transport, and signaling. However, very few auxin pathway genes have been functionally characterized for their role in stress responses in maize, leaving a large knowledge gap in the field. In this review we will describe our current understanding of relationships between auxin and a myriad of stresses, including temperature, drought, salinity, light, and heavy metals. Resilience to environmental stresses is critical for informing agricultural strategies to improve maize yield and quality. We conclude with a discussion of possible future directions and approaches that may increase our understanding of how auxin mediates growth–stress trade-offs in maize.

Keywords: Abiotic stress, auxin, drought, heavy metals, light, maize, salinity, temperature.

Introduction

Abiotic stress is the detrimental effect of abiotic, or non-living, factors on a plant. They are often adverse environmental conditions, including drought, extreme temperatures, or flooding (H. Zhang *et al.*, 2022; Zhang *et al.*, 2023). There are a range of optimal environmental conditions in which plants can grow, and conditions outside this range can negatively impact plant growth and yield. Still, the demand for food will increase with the growing population, which is predicted to exceed 11 billion people by 2100 (Sadigov, 2022). Understanding the basis of abiotic stress in plants can lead to improved strategies in engineering stress-resilient high-yield crops.

Hormones such as jasmonic acid, salicylic acid, brassinosteroids, and striglolactones have been classically associated with abiotic stress responses in plants (Zheng *et al.*, 2022). In contrast, auxin is a classical phytohormone that is typically associated with key roles in modulating plant growth and development. Typically, hormones are hypothesized to influence plant growth in the face of stress, which is often termed a 'growth–stress balance' that results in trade-offs to plant yield (Chen *et al.*, 2021; Ding and Yang 2022). An emerging body of work in model plants and crops has implicated auxin pathways in numerous abiotic stress responses, including Arabidopsis, rice, and horticultural plants. These findings have been recently reviewed in several publications (Q. Zhang *et al.*, 2022; Gupta *et al.*, 2023; Sharma and Marhava 2023; Song *et al.*, 2023; Liu *et al.*, 2024b; Salehin, 2024). In this review, we highlight the recent findings on the role of auxin and numerous abiotic stress responses in maize, namely salt, drought, cold, heat, and heavy metal stress. The focus on highlighting connections between auxin and abiotic stress responses in maize is motivated by the timely research discoveries and their potential impact on global food security. Altogether these new studies suggest that in addition to the growth–stress balance mechanism, auxin may also directly mediate stress responses.

Salt stress responses involve auxin transport and biosynthesis

Approximately a third of irrigated land worldwide is negatively impacted by salinization, equal to 70 Mha, and this area is projected to expand at a rate of 1.0–1.2 Mha annually (Hopmans *et al.*, 2021). Elevated salt concentrations in farmland can occur by many mechanisms and negatively impact yield. For example, rising sea levels degrade coastlines and introduce salt to soil and freshwater sources that support irrigated farmland (Gould *et al.*, 2020). Additionally, increasing temperatures can cause fields to dry out faster and concentrate salts carried in via water irrigation. Most maize species can only tolerate low or mild salt stress (Farooq *et al.*, 2015). Salt treatments as low as 100 mM NaCl can lead to loss in growth (Cao *et al.*, 2023). There are many mechanisms that plants employ in response to salt, including ion regulation, transpiration reduction, osmotic substance accumulation, reactive oxygen species (ROS)-scavenging mechanisms, and hormone mediation (Yu *et al.*, 2020; Cao *et al.*, 2023). Recent genetic studies implicate auxin biosynthesis, transport, and signaling during salt stress responses in maize (Fig. 1A).

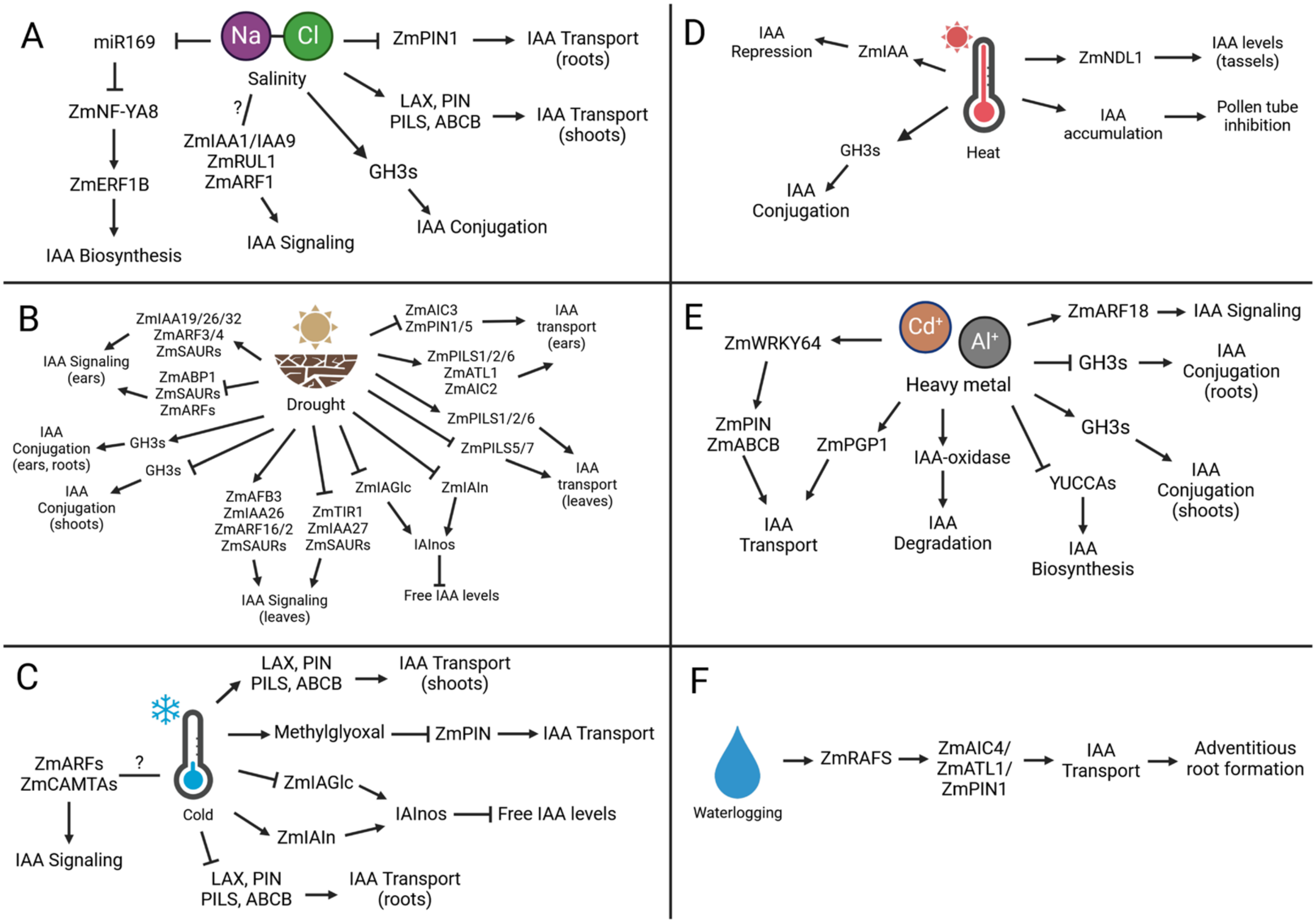

Fig. 1. Distinct and overlapping auxin pathways underpin abiotic stress responses in maize. (A) During salt stress, gene expression changes in auxin signaling proteins, biosynthetic enzymes, and transporters result in an up-regulation of numerous auxin pathways and suppression of auxin transport. (B) Drought stress can elicit a suite of auxin pathway changes via transcription factor activity and metabolic enzymes in vegetative and reproductive tissues. (C) Cold stress is mediated by AUXIN RESPONSE FACTOR (ARF) activity and leads to altered auxin metabolism and transport. (D) Heat stress can influence free indole-3-acetic acid (IAA) levels in tassels and during pollen germination. In other tissues, heat stress can lead to increased auxin inactivation and repression via Aux/IAA action. (E) Heavy metals such as aluminum (Al^{+}) and cadmium (Cd^{+}) can alter auxin transport, signaling, and biosynthesis. (F) Waterlogging can promote adventitious root formation via activation of raffinose and increasing IAA levels. Created in BioRender. Kelley, D. (2025) https://BioRender.com/s50x605.

Auxin biosynthesis is regulated in response to salt stress in maize. Changes in the expression of genes related to auxin biosynthesis during salt stress have been observed in multiple studies. Overexpression or activation of YUCCAs, key auxin biosynthetic genes, can increase salt tolerance in some species (Yan *et al.*, 2016; Xu *et al.*, 2018; Cackett *et al.*, 2022). Auxin biosynthesis can be promoted through ZmERF1B activation via ZmNF-YA8 binding. However, miR169 can bind to ZmNF-YA8, thus preventing ERF1B activation. Salt stress inhibits transcription of miR169, thus increasing auxin biosynthesis and accumulation (Xing *et al.*, 2023). Auxin levels can also change through auxin inactivation and degradation. Salt can induce most auxin-conjugating glycoside hydrolase 3 (GH3) enzymes to mediate free auxin levels (Feng *et al.*, 2015). In addition to auxin biosynthesis, auxin transport is differentially regulated in response to salt stress. Salt stress up-regulates auxin transport families (LAX, PIN, PILS, and ABCB) in shoots, although these genes are typically down-regulated in roots (Yue *et al.*, 2015). Abscisic acid induced during salt stress disrupts localization of ZmPIN1 in lateral roots and prevents lateral root formation (Lu *et al.*, 2019). These results indicate that auxin biosynthesis, metabolism, and transport are regulated to change auxin accumulation during salt stress.

Auxin signaling is also involved in salt stress response in maize. Quantitative trait locus (QTL) analysis has identified ZmIAA1 and ZmRUL1 as candidate genes controlling root plasticity during salt stress (Li *et al.*, 2021). Overexpression of ZmARF1 in Arabidopsis can confer salt tolerance, as ARF1 targets peroxidase genes to regulate ROS production during stress (Liu *et al.*, 2024a). However, ZmIAA9 can positively regulate salt tolerance through repression of ZmARF1 (Yan *et al.*, 2023). More research is needed to fully elucidate the role of auxin signaling in maize salinity response.

Auxin signaling and transport are implicated in drought responses

Drought stress is caused by low rainfall and decreased water availability, but increased temperature, high light intensity, and even dry wind can exacerbate these conditions (Seleiman *et al.*, 2021). Drought is one of the most detrimental natural occurrences in agriculture. In the USA, drought events from 2014 to 2023 caused losses worth over US$50.3 billion (NCEI, 2024). Drought response varies in sink tissues, such as leaves, when compared with source tissues (such as the ear and the kernel) (Wang *et al.*, 2019). Overall, the maize response to drought stress is finely tuned on an organ-specific level through auxin signaling, transport, and biosynthesis (Fig. 1B). As described in more detail below, numerous examples from the literature indicate that drought may positively or negatively influence the expression of auxin pathway genes. This mixed bag of expression patterns makes it difficult currently to draw any overall conclusions about the relationships between auxin genes and drought response in maize.

In kernels and ears, the auxin signaling cascade is greatly altered during drought stress. Numerous genes encoding members of the Aux/IAA family (IAA26, IAA32, and IAA19) are up-regulated in both kernels and ears, while those encoding AUXIN BINDING PROTEIN1 (ABP1) and SMALL AUXIN UPREGULATED (SAUR) are down-regulated (Wang *et al.*, 2019). In kernels, several ARF and SAUR family members are down-regulated. In leaves, AFB3, IAA26, ARF16/2, and some SAURs are up-regulated in response to drought stress. TIR1, IAA27, and some SAURs are down-regulated (Wang *et al.*, 2019).

In maize seedlings, multiple ARF and Aux/IAA family proteins are up-regulated in drought conditions (Seeve *et al.*, 2017). ZmARF1 targets peroxidase genes to regulate ROS production during stress (Liu *et al.*, 2024a). Recently, the disease resistance gene *ZmCCT* has been shown to confer drought tolerance when overexpressed through interaction with *ZmIAA8* (Zhang *et al.*, 2024). In the osmotic stress-resistant maize mutant *osr1*, transcripts for various auxin response genes were significantly up-regulated (ARF3, ARF4, and SAURs) (Han *et al.*, 2024). Future investigation into the links between these different genes and drought responses will be needed to better understand the collective roles of transcriptional responses during these processes.

Additionally, auxin transport is modified during drought response in maize. In ears, auxin influx transporter genes (*AIC3* and *AIC4*) are down-regulated, while an auxin efflux gene (*PILS6*) is up-regulated (Wang *et al.*, 2019). In kernels, several auxin transporters (ATL1, AIC2, AIC4, PIN1, and PIN5) are down-regulated while auxin biosynthetic genes are up-regulated. In leaves, PILS1, PILS2, and PILS6 are up-regulated in response to drought stress, while PILS5 and PILS7 are down-regulated (Wang *et al.*, 2019).

Free indole-3-acetic acid (IAA) is the bioactive form of the molecule yet comprises only up to 25% of the auxin pool (Ludwig-Müller, 2011). The majority of the auxin pool is made up of IAA conjugated to sugars, amino acids, or proteins (Woodward and Bartel, 2005; Bajguz and Piotrowska, 2009). Many conjugates are either degraded or stored for later use, but some auxin conjugates have potential roles outside of regulating levels of free IAA (Staswick, 2009; Ludwig-Müller, 2011; González-Lamothe *et al.*, 2012). Free auxin levels are also modulated in response to drought. Enzymes that make indole-3-acetyl-*myo*-inositol (IAInos), an inactive form of auxin that has been conjugated to *myo*-inositol, are inactivated during drought stress to increase free auxin levels (Ciarkowska *et al.*, 2022). Drought treatment [polyethylene glycol (PEG)] induces GH3 expression in roots but reduces expression in shoots (Feng *et al.*, 2015). GH3 expression is induced in ears during drought stress (Seeve *et al.*, 2017).

Cold stress in maize is linked to several auxin pathways

Cold stress (or chilling stress) occurs during temperatures between 0 °C and 15 °C. Plants native to cold areas have cold acclimation strategies, such as modifying cell membranes, altering protein and sugar synthesis, and accumulating osmolytes (Theocharis *et al.*, 2012; Satyakam *et al.*, 2022). However, tropical and subtropical plants, such as rice, maize, soybean, cotton, and tomato, are sensitive to cold stress. This temperature constraint limits where certain crops can be grown, thus understanding the mechanisms behind the cold stress response could be a key target in the future.

Maize is sensitive to cold stress at all stages of development, from germination to kernel formation (Majláth *et al.*, 2022; Goering *et al.*, 2021). Several studies indicate a link between plant metabolism and auxin following cold stress. During cold exposure, compounds that lead to oxidative stress can form and trigger a defense response. This can include the reactive aldehyde methylglyoxal (MG). A study on the effects of MG on maize seeds found that it can improve germination rates and photosynthetic performance when the plants are grown under low temperature. In addition, transcriptomic analysis of MG-induced changes in maize identified a decrease in auxin transporter expression (Majláth *et al.*, 2022). This study proposes that MG can act as a signal to pre-condition maize plants to cold stress, which is ameliorated by changes in hormones (including auxin).

Another metabolite that is regulated by cold during seedling development is IAInos (Ciarkowska *et al.*, 2022). In germinating maize seeds, IAInos biosynthesis increases in coleoptiles and radicles. Under cold stress, the activity of enzymes that produce IAInos decreases in seeds and increases in coleoptiles, while free IAA levels remain unchanged. Raffinose can mitigate cold stress, and lead to changes in IAA abundance (Yan *et al.*, 2024). Thus, the levels of free IAA are dynamically regulated in kernels in response to cold in combination with several other metabolites.

In tropical regions, low soil temperature during planting can negatively impact maize kernel germination. A recent study examined the interplay between microbes, cold stress, and auxin to determine if growth-promoting bacteria could be beneficial to improve cold tolerance. Treatment of maize plants with microbes supplemented with zinc (Zn) and manganese (Mn) led to increased shoot IAA, root length, and shoot biomass. Thus, synergistic interactions between microbes, auxin, and nutrients may be beneficial for cold tolerance in maize (Moradtalab *et al.*, 2020).

QTL mapping for cold-tolerant loci in maize identified two regions controlling cold tolerance variation (Goering *et al.*, 2021). Underlying these two QTLs are two auxin-responsive family genes as candidate genes, suggesting that the auxin response could contribute to chlorophyll concentration, leaf color, and/or tissue damage during cold stress in maize (Goering *et al.*, 2021). In addition, transcriptomic analyses have determined that numerous auxin transporters are regulated by cold (Yue *et al.*, 2015). Calmodulin-binding transcription activators (CAMTAs) play critical roles in environmental responses and could be strong candidates for mediating cold-responsive activation of auxin pathway genes. CAMTAs in maize (termed ZmCAMTAs) have been examined for their expression patterns, and several ZmCAMTA family members are regulated by both cold and auxin treatment (Yue *et al.*, 2015). Additional investigation into the functional significance of these transcription factors and their targets will be required to better understand how they influence cold tolerance downstream of auxin (Fig. 1C).

Heat can promote and repress maize growth via auxin

Global temperature is predicted to increase by 1.5 °C by 2033–2035 (Diffenbaugh and Barnes, 2023). When plants are exposed to heat >5 °C above their optimal growing conditions, they exhibit signs of heat stress, including membrane damage, biomass reduction, and inactivation of photosynthetic enzymes (Bita and Gerats, 2013; Mishra *et al.*, 2023).

In vegetative organs, heat can either promote or repress growth (Bianchimano *et al.*, 2023). Leaf elongation in maize increases between 4 °C and 30 °C but declines at higher temperatures (Parent and Tardieu, 2012). Another study found that in maize leaves, auxin levels increase in the heat-sensitive cultivar SHEMAL following a heat treatment but were unchanged in a heat-tolerant cultivar, MAY 69 (Dinler *et al.*, 2014). Ascorbate treatment under heat stress also led to an increase in IAA levels in SHEMAL leaves at 4 h, but not 8 h (Dinler *et al.*, 2014). These data suggest that heat-tolerant maize cultivars may be buffered against fluctuating IAA levels, while heat-sensitive cultivars exhibit rapid and transient increases of IAA.

In reproductive tissues, links between auxin and heat stress have been identified from genetic and expression analyses. A key gene involved in thermotolerance and inflorescence meristem development is *NEEDLE1*, which encodes a mitochondria-localized ATP-dependent metalloprotease (Liu *et al.*, 2019). Genetic analyses of *ndl1* in combination with *Bif1*, a stabilized Aux/IAA mutant, and *spi1*, an auxin biosynthetic mutant, indicated that auxin levels may be altered in *ndl1* inflorescences (Liu *et al.*, 2019). In the absence of NDL1, auxin levels were lower in tassels compared with the wild type, and seedling roots were insensitive to exogenous auxin treatment (Liu *et al.*, 2019). Altogether, this work established that heat-induced production of ROS can influence auxin pathways and impair organ formation.

Heat stress has long been associated with negative impacts on pollen viability in maize (Schoper *et al.*, 1987; Waqas *et al.*, 2021; Liu *et al.*, 2023). A recent study determined that pollen tube growth rather than germination was impaired during heat stress (Wang *et al.*, 2023), but previous work has also indicated that heat stress induces meiotic defects and/or premature spore abortion (Begcy *et al.*, 2019). Significant increases in auxin levels were observed coincident with heat-induced pollen tube inhibition, suggesting that hormone levels are directly impacted by increased temperature (Wang *et al.*, 2023). High temperature can also impair kernel development and starch deposition in maize (Guo *et al.*, 2021). A multi-omics analysis of heat-treated kernels determined that auxin signaling pathways were active at 10 d after pollination but not at 25 d (Guo *et al.*, 2021). Increases in auxin production under high temperature have also been reported for other organs and plant species (Gray *et al.*, 1998). Future investigation into the transcription factors and enzymes that underpin these responses in maize will be needed to further delineate how these changes are carried out within various tissues (Fig. 1D).

Heavy metal tolerance in maize may impact auxin metabolism and transport

Heavy metals are toxic to plants. They are absorbed in their ion form and can cause oxidative damage. Heavy metal is becoming an issue because of industrial pollution (Obaid *et al.*, 2023). Solubilized aluminum is easily taken up by plant roots and transported to all parts of the plant (Anjum *et al.*, 2016). Aluminum stress occurs at levels of 60 μM and can lead to reduced root growth, cell death, and leaf necrosis (Anjum *et al.*, 2015; Malekzadeh *et al.*, 2015; Du *et al.*, 2020). Cadmium (Cd) stress can occur at levels of 75 μM (Anjum *et al.*, 2015). Cd can be translocated to shoots and affects the whole plant (Małkowski *et al.*, 2020). Plants suffering from Cd toxicity show a variety of symptoms, including a reduced rate of photosynthesis, decreased nutrient uptake, and inhibited growth (Haider *et al.*, 2021). Thus, the effects of various heavy metals on maize development are relevant for improving agriculture.

Auxin biosynthesis and transport are affected by heavy metal stress (Fig. 1E). Aluminum stress activates ZmPGP1 to reduce auxin accumulation at root tips (Zhang *et al.*, 2018). In response to acidic soil and aluminum, auxin response genes and tryptophan biosynthetic genes are up-regulated (Mattiello *et al.*, 2014). Studies on the influence of Cd on auxin pathways are more complicated and it is difficult to discern consistent responses. For example, Cd treatment induces GH3 expression in shoots but reduces expression in roots, which may

Table 1. Recent findings on auxin responses during maize abiotic stress responses

Stress	Organ	Mechanism	References
Salinity	Root	- Increased auxin biosynthesis - Reduced auxin transport - GH3s induced	Xing *et al.* (2023) Lu *et al.* (2019) Yue *et al.* (2015) Feng *et al.* (2015)
	Shoot	- Increased auxin transport - GH3s induced	Yue *et al.*(2015) Feng *et al.* (2015)
Drought	Kernels/Ears	- Decreased ARF, SAUR, ABP1 expression, increased Aux/IAA, ARF3/4, SAUR expression - Decreased PIN, AIC3 expression, increased PILS, ATL, AIC2 expression - GH3s induced	Wang *et al.* (2019) Han *et al.* (2024) Seeve *et al.* (2017)
	Leaves	- Increased ARF, SAUR, AFB, IAA26 expression, decreased TIR1, IAA27, SAUR expression - Increased PILS1/2/6 expression, decreased PILS5/7 expression	Wang *et al.* (2019) Zhang *et al.* (2024) Ciarkowska *et al.* (2022)
	Shoot	- GH3s repressed	Feng *et al.* (2015)
	Root	- GH3s induced	Feng *et al.* (2015)
Cold	Root	- Reduced auxin transport	Yue *et al.* (2015)
	Shoot	- Increased auxin transport - Altered IAA signaling	Yue *et al.* (2015) Majláth *et al.* (2022) Goering *et al.* (2021)
	Seedling	- Altered free IAA	Ciarkowska *et al.* (2022) Yan *et al.* (2024)
Heat	Tassel	- Auxin levels increased	Liu *et al.* (2019) Dinler *et al.* (2014)
	Pollen tube	- Auxin levels increased	Wang *et al.* (2023)
	Kernel	- Increased Aux/IAA expression - GH3s induced	Guo *et al.* (2021)
Heavy metal	Root	- Increased auxin transport - Decreased auxin biosynthesis - Increased auxin signaling - Increased auxin degradation - GH3s repressed	Zhang *et al.* (2018) Gu *et al.* (2024) Yue *et al.* (2016) Mattiello *et al.* (2014) Feng *et al.* (2015)
	Shoot	- GH3s induced	Feng *et al.* (2015)
Waterlogging	Root	- Increased auxin levels - Increased auxin transport	Yan *et al.* (2024)

reduce free auxin levels during Cd stress (Feng *et al.*, 2015). The YUCCA family of auxin biosynthetic genes were down-regulated after Cd treatment, while IAA-oxidases had increased expression (Yue *et al.*, 2016). An additional study found that exogenous treatment with indole 3-butyric acid (IBA) led to higher endogenous IAA levels and modified cell wall composition with sequestered Cd (Šípošová *et al.*, 2023). Finally, it has been reported that auxin transport is up-regulated by heavy metal stress. Specficially, the expression of ABCB and PIN family members is increased via activation of ZmWRKY64 under Cd stress (Gu *et al.*, 2024). The overall impacts of simultaneous changes to auxin biosynthesis, metabolism, and transport during heavy metal exposure will need to be further evaluated in vegetative tissues.

Waterlogging can induce auxin biosynthetic genes

Waterlogging stress occurs when a plant's root zone is fully submerged in water (Sasidharan *et al.*, 2017). Flooding around the root system halts gas exchange, leading to decreased rates of

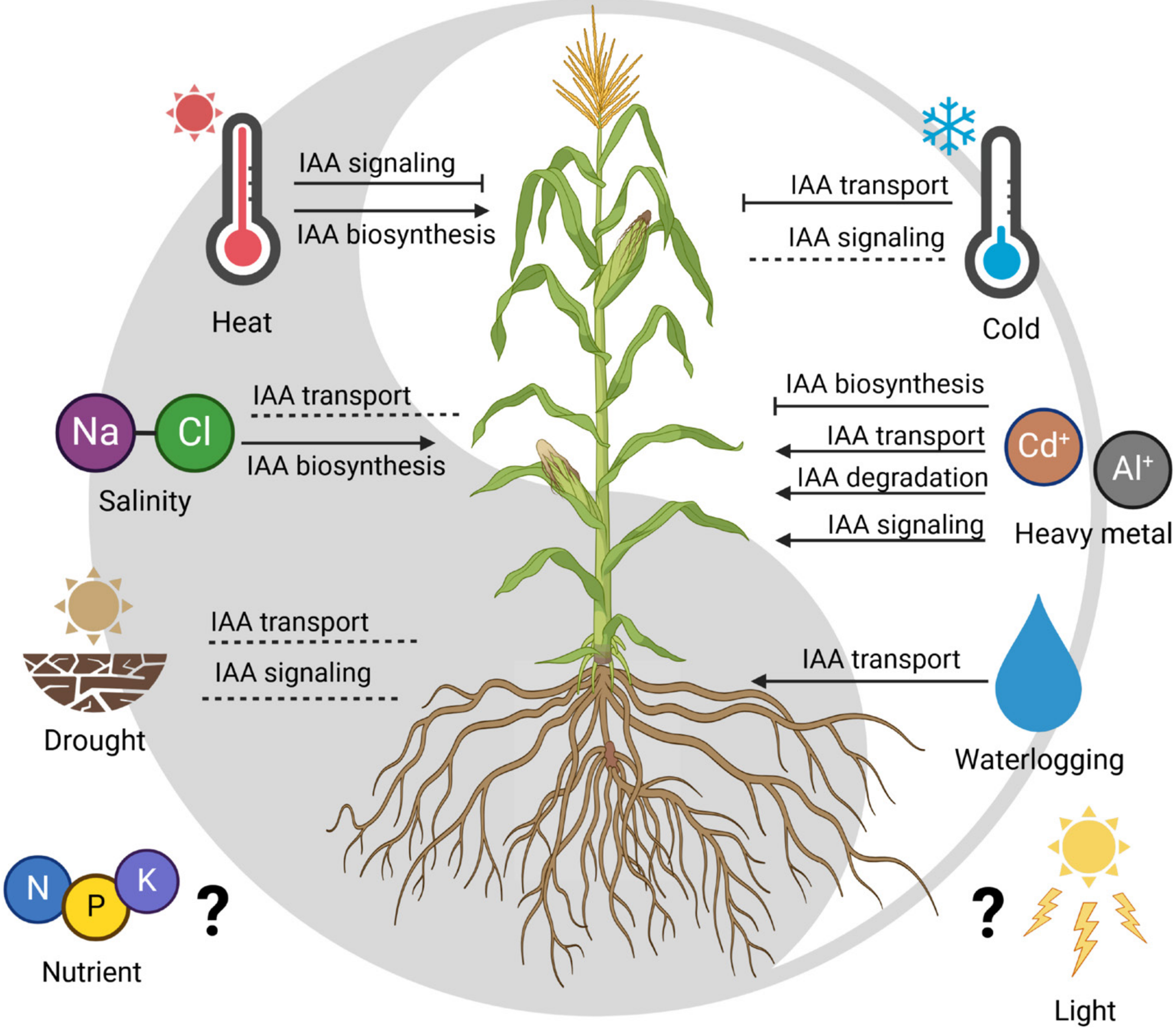

Fig. 2. Auxin plays a role in numerous abiotic stress responses in maize. Solid lines represent literature-supported relationships. Dashed lines represent unknown pathways. Auxin acts as a negative regulator of heat, salinity, and drought stress. During heat stress, auxin signaling is impaired while auxin biosynthesis is promoted. Both salt and drought stress can promote or repress auxin transport in a tissue-specific manner and increase auxin biosynthesis. Drought stress regulates auxin signaling in a tissue-specific manner. Auxin is a positive regulator of cold, heavy metal, and waterlogging stress. Cold stress represses auxin biosynthesis and transport. Some auxin-responsive transcription factors are also regulated by cold but need further study. Heavy metal stress inhibits auxin biosynthesis but increases auxin transport. Waterlogging stress induces auxin biosynthesis. The direct roles of auxin pathways in light stress and/or nutrient stress responses in maize are not well established. Created in BioRender. Kelley, D. (2025) https://BioRender.com/d94z363.

cellular respiration and photosynthesis (Manghwar *et al.*, 2024). This, in turn, can cause root death, oxidative damage, and leaf senescence (Manghwar *et al.*, 2024). Short-term waterlogging stress can have lasting impacts on plant growth and development. For example, waterlogging stress for as few as 3 d can lead to reduced growth in wheat (Francioli *et al.*, 2021).

Waterlogging stress can lead to increased adventitious root and aerenchyma formation in maize (Yan *et al.*, 2024). Raffinose is a key metabolite that can provide waterlogging tolerance (Yan *et al.*, 2024). In this same study, transcriptome analysis of *zmrafs-1* indicated that auxin biosynthetic genes are up-regulated by raffinose. During waterlogging, increased levels of raffinose lead to increased levels of IAA, which in turn can lead to adventitious root formation and increased tolerance (Yan *et al.*, 2024) (Fig. 1F). Given the increasing incidents of flooding in maize fields due to extreme weather events (Toulotte *et al.*, 2022; Du and Xiong 2024; Yildirim and Demir 2022; Sinha *et al.*, 2024; Song *et al.*, 2022; Arunrat *et al.*, 2022; Gallé *et al.*, 2020), additional investigation into links between auxin and waterlogging would be of relevance to the community.

Conclusions and future directions

Maize is a key cereal crop that is grown worldwide and is subjected to a myriad of abiotic stresses. We provide a summary of the notable results in Table 1 and key auxin-related processes in Fig. 2. The extensive genetic diversity of maize indicates that genotype differences may influence abiotic stress tolerance via auxin pathways. Continued research into the connections between auxin and light stress in field-grown adult maize plants can be investigated using improved phenotyping approaches and functional genomics, which could be investigated using genetic approaches. In addition, the links between auxin and nutrient stress have not been described yet. Overall, many of the reported studies on abiotic stress in maize implicate rapid changes in free IAA levels, suggesting that auxin biosynthetic and/or metabolic pathways are a common regulatory module following abiotic stress exposure in maize. Thus, genetic strategies to improve tolerance to pressing abiotic stresses (i.e. drought, temperature, and salinity) exacerbated by climate change could leverage auxin biosynthesis, metabolism, or transport candidate genes as potential influencers in maize.

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Author contribution

CFG and DRK: conceptualization, writing—original draft, review & editing; CFG: visualization; DRK: funding acquisition.

Conflict of interest

The authors have no conflicts of interest to declare.

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