

REVIEW PAPER

Auxin and abiotic stress responses

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Abstract

Plants are exposed to a variety of abiotic stresses; these stresses have profound effects on plant growth, survival, and productivity. Tolerance and adaptation to stress require sophisticated stress sensing, signaling, and various regulatory mechanisms. The plant hormone auxin is a key regulator of plant growth and development, playing pivotal roles in the integration of abiotic stress signals and control of downstream stress responses. In this review, we summarize and discuss recent advances in understanding the intersection of auxin and abiotic stress in plants, with a focus on temperature, salt, and drought stresses. We also explore the roles of auxin in stress tolerance and opportunities arising for agricultural applications.

Keywords: Abiotic stress, auxin, drought, phytohormone, salt, temperature.

Introduction

Plants cope with constantly changing environments that are often stressful or unfavorable for their growth. Thus, they have evolved the capacity to survive under wide-ranging abiotic stresses. However, the frequency and severity of these encountered stresses are increasing because of climate change, with deleterious effects on plant growth and crop productivity (reviewed in Hamann *et al.*, 2021). Commonly encountered abiotic stressors include heat, salt, drought, cold, nutrient deficiency, and toxic metals (reviewed in Zhu, 2016). Amongst these abiotic stresses, extreme temperatures, salt, and drought are environmental factors that hinder plant growth, geographical distribution, and crop productivity (reviewed in Waadt *et al.*, 2022). Plant survival under these environmental stresses requires sophisticated regulatory pathways that facilitate withstanding adverse growth conditions. Genetic, biochemical, and molecular studies have identified numerous

factors that regulate abiotic stress responses, involving stress sensing, transcription, and signal transduction (reviewed in Zhang *et al.*, 2022). Amongst these factors, many plant hormones mediate abiotic stress adaptation (reviewed in Waadt, 2020); in this review, we focus on the roles of the phytohormone auxin in abiotic stress.

Auxin is a master regulator of plant growth and development through its control of cell division, elongation, and differentiation. Fundamental auxin responses are divided into three major pathways: metabolism, transport, and signal transduction. Recent work on the biochemical, genetic, and structural aspects of auxin has resulted in an increased understanding of the interplay of auxin–stress responses. In this review, we discuss recent progress in our understanding of the roles of auxin in abiotic stress, especially drought, salt, and extreme temperatures.

Brief overview of auxin

The name ‘auxin’ is derived from the Greek word ‘auxein’ meaning ‘to grow or to expand’, which indicates that the critical effects of auxin are on plant growth (reviewed in [Abel and Theologis, 2010](#)). Over a century of studies have revealed that the regulation of plant growth and development is largely executed via coordination of auxin metabolism, auxin translocation, and auxin response (reviewed in [Enders and Strader, 2015](#)). Auxin biosynthesis and function are involved in response to abiotic stresses, such as heat, salt, drought, and cold.

Auxin metabolism

Indole-3-acetic acid (IAA) is the best-studied naturally occurring active auxin in plants. Research on auxin metabolism has established that the aromatic amino acid L-tryptophan (Trp) is the central precursor for IAA biosynthesis in plants (reviewed in [Enders and Strader, 2015](#)). Several decades of studies indicate that auxin levels are regulated by its biosynthesis and

inactivation ([Fig. 1](#)), which are extensively involved in the heat, salt, drought, and cold stresses (reviewed in [Casanova-Saez et al., 2021](#)).

Auxin biosynthesis

Generating auxin from Trp is considered the main route of IAA biosynthesis (reviewed in [Zhao, 2018](#)). Several Trp-dependent auxin biosynthetic routes have been proposed, including the IAOx (indole-3-acetaldoxime), IAM (indole-3-acetamide), and IPyA (indole-3-pyruvic acid) pathways (reviewed in [Casanova-Saez et al., 2021](#)). Whereas the IAOx and IAM pathways are not fully understood, the IPyA pathway has been established as the main contributor to IAA synthesis and is the only completely described pathway to date (reviewed in [Cao et al., 2019](#)). The IPyA pathway consists of a two-step reaction: the TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA) family of enzymes converts Trp to IPyA, and then the YUCCA (YUC) family of enzymes converts IPyA to IAA (reviewed in [Casanova-Saez et al., 2021](#)). Trp is deaminated into IPyA by TAA1 and TAA1-RELATED proteins (TARs).

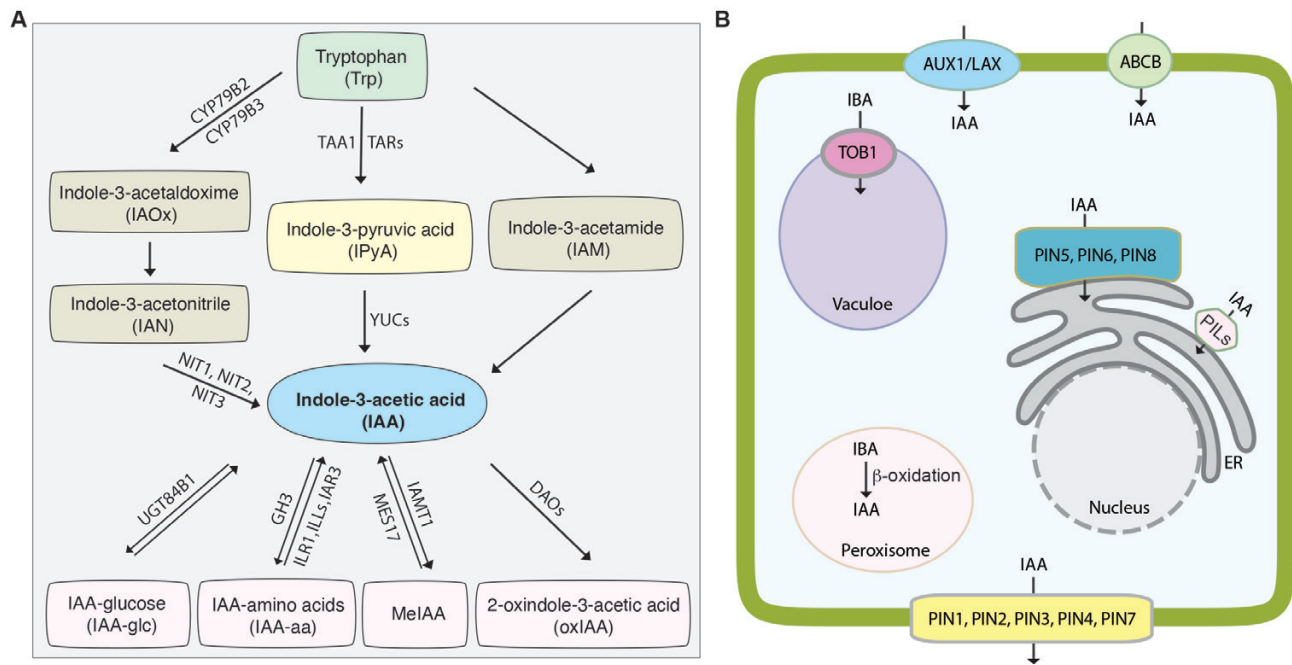


Fig. 1. The central pathways for auxin biosynthesis, inactivation, and transport in plants. (A) The primary routes for auxin biosynthesis and inactivation. Indole-3-acetic acid (IAA), as a naturally occurring active auxin, is synthesized from the main precursor L-tryptophan (L-Trp). The Trp-dependent pathways comprise the indole-3-acetaldoxime (IAOx), the indole-3-acetamide (IAM), and the indole-3-pyruvic acid (IPyA) pathways. Amongst these pathways, the IPyA route is considered to be the main contributor to IAA synthesis. In addition to auxin biosynthesis, auxin levels are also regulated by its inactivation through conjugation and degradation. There are three reversible auxin conjugates: ester-linked IAA, amide-linked IAA, and methyl IAA. Irreversible auxin degradation is through the oxidation of IAA to 2-oxindole-3-acetic acid (oxIAA) by the dioxygenase for auxin oxidation (DAO). (B) The intercellular auxin distribution is established by the influx and efflux carriers. AUXIN RESISTANT1/LIKE AUX1 (AUX1/ LAX) transporters facilitate the influx of IAA. PIN-FORMED (PIN) and ATP-BINDING CASSETTE SUBFAMILY B (ABCB) protein families facilitate the efflux of IAA. The long canonical PIN proteins, PIN1, PIN2, PIN3, PIN4, and PIN7, are polarly localized to the plasma membrane (PM). The short non-canonical PIN proteins, PIN5, PIN6, and PIN8, localize to the endoplasmic reticulum (ER) membrane. PIN-LIKES (PILS) proteins are ER localized and contribute to intracellular auxin transport. In addition, the transporters of auxin precursor indole 3-butyric acid (IBA), that is converted to IAA by a β -oxidation in peroxisome, mediates auxin metabolism.

IPyA is then decarboxylated in an irreversible reaction catalyzed by the YUC family of flavin-containing monooxygenases to produce IAA (reviewed in [Cao *et al.*, 2019](#)). TAA1 and YUC homologs are found across the plant kingdom, and the role of the TAA/YUC pathway is fully supported by genetic and biochemical evidence, suggesting that the Trp-dependent IPyA pathway is a universal route for IAA biosynthesis in plants (reviewed in [Morffy and Strader, 2020](#)).

Auxin inactivation

In addition to the local auxin biosynthesis, auxin levels are modulated by metabolic inactivation through conjugation and degradation. Reversible formation of auxin conjugates provides a mechanism for rapid regulation of active auxin levels. Three major auxin storage forms have been identified, namely ester-linked IAA, amide-linked IAA, and methyl IAA (reviewed in [Casanova-Saez *et al.*, 2021](#)). IAA-glucose (IAA-Glc) is the predominant ester-linked auxin conjugate ([Pencik *et al.*, 2018](#); [Brunoni *et al.*, 2020](#)). Amide linkages are formed when auxin is conjugated by amino acids and small peptides. IAA-amino acids are major amide conjugates whose formation is catalyzed by products of the *GRETCHEN HAGEN3 (GH3)* family genes ([Staswick *et al.*, 2005](#); [Ludwig-Muller *et al.*, 2009](#)). Moreover, IAA can also be converted to the methyl ester form MeIAA, which is mediated by *IAA CARBOXYMETHYLTRANSFERASE1 (IAMT1)* ([Zubieta *et al.*, 2003](#); [Qin *et al.*, 2005](#)). In addition to inactivation of auxin by conjugation, auxin degradation also regulates IAA levels, frequently through the irreversible oxidation of IAA to 2-oxindole-3-acetic acid (oxIAA) ([Kubes *et al.*, 2012](#); [Pencik *et al.*, 2013](#)). The *DIOXYGENASE FOR AUXIN OXIDATION (DAO)* gene product catalyzes the conversion of IAA to oxIAA ([Zhao *et al.*, 2013](#)). IAA levels can also be regulated by the chain-lengthened precursor indole-3-butyric acid (IBA), which is converted into active IAA through a β -oxidation process (reviewed in [Damodaran and Strader, 2019](#)).

Auxin transport

Auxin forms local concentration minima, maxima, or gradients between cells to drive developmental events ([Fig. 1](#)). Auxin concentration gradients are established by a directional cell-to-cell transport (reviewed in [Hammes *et al.*, 2022](#)). Plasma membrane-based influx and efflux carriers control intercellular auxin distribution (reviewed in [Sauer and Kleine-Vehn, 2019](#)). Members of the AUXIN RESISTANT1/LIKE AUX1 (AUX1/LAX) transporters facilitate the influx of IAA, whereas members of the PIN-FORMED (PIN) and ATP-BINDING CASSETTE SUBFAMILY B (ABCB) protein families facilitate the efflux of IAA. In parallel, transporters of the auxin precursor IBA can fine-tune auxin levels to affect plant development (reviewed in [Damodaran and Strader, 2019](#); [Michniewicz *et al.*, 2019](#)). Recent evidence suggests that auxin

transport from local biosynthesis and storage forms plays essential roles during heat, salt, drought, and cold stresses.

Auxin influx

To date, four auxin influx carriers with specific functions have been described in Arabidopsis, namely AUX1, LAX1, LAX2, and LAX3 (reviewed in [Swarup and Bhosale, 2019](#)). The diversity of mutant phenotypes displayed in mutants defective in *AUX/LAX* family members reveals distinct function for these auxin carriers ([Bennett *et al.*, 1996](#); [Bainbridge *et al.*, 2008](#); [Swarup *et al.*, 2008](#); [Péret *et al.*, 2012](#); [Moreno-Piovanio *et al.*, 2017](#)). Altogether, these AUX1/LAX influx carriers play critical roles for auxin transport to regulate plant development.

Auxin efflux

PIN and ABCB family members are auxin efflux carriers. In Arabidopsis, there are eight PINs with conserved N- and C-terminal domains and less conserved hydrophilic loops ([Nodzynski *et al.*, 2016](#)). The length of hydrophilic loops divides PINs into two classes, 'long' canonical PINs and 'short' or 'intermediate' non-canonical PINs (reviewed in [Bogaert *et al.*, 2022](#)). Long canonical PIN proteins include PIN1, PIN2, PIN3, PIN4, and PIN7, which are polarly localized to the plasma membrane ([Adamowski and Friml, 2015](#)). Canonical PINs are polarly distributed in different cell types ([Adamowski and Friml, 2015](#); reviewed in [Hammes *et al.*, 2022](#)). Canonical PINs are necessary to establish differential distribution of auxin to regulate aspects of plant growth and stress responses. In parallel, ABCB protein transporters also mediate auxin efflux and play roles in plant development ([Chen *et al.*, 2023](#); reviewed in [Hao *et al.*, 2020](#); [Hammes *et al.*, 2022](#)).

Auxin signal transduction

Over the past three decades, extensive genetic and biochemical studies have elucidated the mechanisms of auxin signaling. The major nuclear mechanism for auxin-mediated gene expression is based on the TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING F-BOX PROTEINS (TIR1/AFBs) pathway. Additionally, the non-canonical transmembrane kinase (TMK) and extranuclear TIR1/AFBs pathway also mediate auxin signal transduction. The auxin signal pathway is essential to heat, salt, drought, and cold responses in plants, as described below.

The canonical TIR1/AFB-AUX/IAA pathway

The TIR1/AFB auxin signal transduction pathway ([Fig. 2](#)) involves three major components: the SCF^{TIR1/AFB} receptors complex, Auxin/INDOLE-3-ACETIC ACID (Aux/IAA) repressor proteins, and AUXIN RESPONSE FACTOR (ARF) transcription factors (reviewed in [Morffy and Strader, 2022](#)). The TIR1/AFBs are F-box proteins that are incorporated into a SKP1-CUL1-F-box (SCF)-type E3 ubiquitin ligase ([Pickart, 2001](#); [Gagne *et al.*, 2002](#)). There are six members of the TIR1/AFB family, with distinct and overlapping

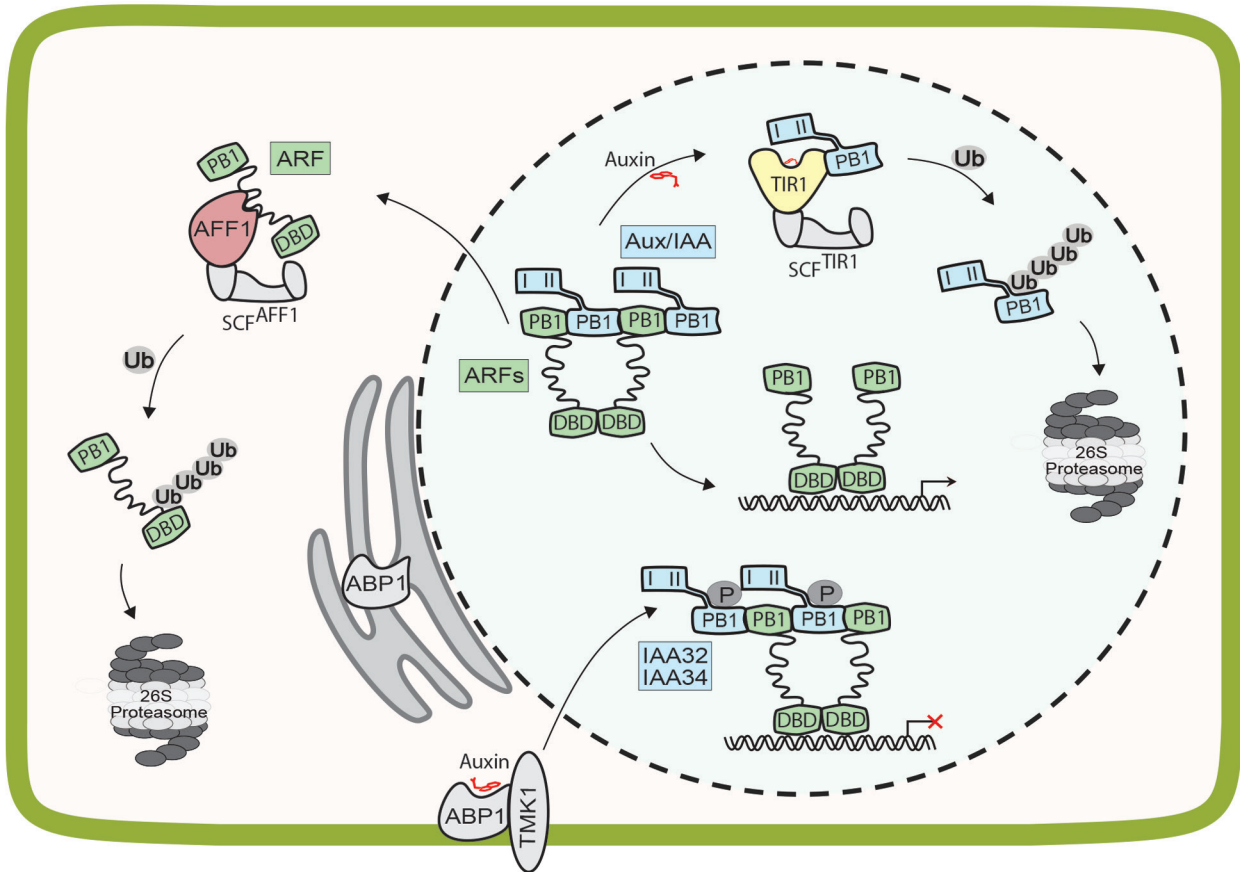


Fig. 2. The central pathways for auxin signal transduction. Nuclear auxin signal transduction is mediated by the TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING F-BOX PROTEINS (TIR1/AFBs) pathway, which includes the AUXIN RESPONSE FACTOR (ARF) transcription factors and Auxin/INDOLE-3-ACETIC ACID (Aux/IAA) repressor proteins. The E3 ubiquitin ligase TIR1/AFBs are complexed with the S PHASE KINASE-ASSOCIATED PROTEIN1 (SKP1) (or ASK1 in plants), CULLIN1 (CUL1), and RING BOX1 (RBX1), forming an SCF^{TIR1/AFB} complex. Aux/IAs interact with ARFs to prevent auxin signaling under low levels of auxin. As the auxin levels increase, auxin induces Aux/IAA binding to the SCF^{TIR1/AFB} complex, causing the ubiquitination and degradation of Aux/IAA proteins through the 26S proteasome. The degradation of Aux/IAA proteins relieves ARF repression to allow ARF-mediated transcription to proceed. In parallel, the E3 ubiquitin ligase AUXIN RESPONSE FACTOR F-BOX1 (AFF1) facilitates the ubiquitylation of ARF7 and ARF19 for degradation through the 26S proteasome, regulating the auxin signaling transduction. Additionally, the transmembrane kinase (TMK) proteins localized in the plasma membrane mediate cell surface auxin signal transduction by binding to the non-canonical IAA32 and IAA34. The auxin-binding protein 1 (ABP1) also mediates auxin signaling through the TMK1-based cell surface pathway.

functions (Parry *et al.*, 2009; reviewed in Salehin *et al.*, 2015). Aux/IAA proteins are transcriptional repressors, which have three major domains: the DI that encodes the repressive domain, DII that encodes the degron, and a type I/II Phox and Bem1 (PB1) domain that mediates the interactions between Aux/IAs and ARFs (reviewed in Morffy and Strader, 2022). ARF transcription factors tightly control auxin responses by either activating or repressing target genes (reviewed in Powers and Strader, 2020). ARFs are divided into three conserved evolutionary classes: class A are considered to be transcriptional activators whereas class B/C are thought to be transcriptional repressors (Okushima *et al.*, 2005; Finet *et al.*, 2013; Mutte *et al.*, 2018). Most ARF proteins contain three regions: an N-terminal B3-type DNA-binding domain (DBD), an intrinsically disordered variable middle region (MR) that functions as either a transcriptional activator or repressor, and a

C-terminal PB1 protein-protein interaction domain (Roosjen *et al.*, 2018). ARF proteins are regulated by the 26S proteasome (Li *et al.*, 2004; Salmon *et al.*, 2008; Lakehal *et al.*, 2019; Jing *et al.*, 2022). The latest discovery of the F-box protein AUXIN RESPONSE FACTOR F-BOX1 (AFF1) that regulates ARF accumulation and nucleo-cytoplasmic partitioning, provides new insights into auxin signal transduction (Jing *et al.*, 2022; Gorska *et al.*, 2023).

Under low auxin conditions, Aux/IAs directly interact with ARFs via the PB1 domain and prevent transcription of auxin-responsive genes. As auxin levels increase, auxin acts as a ‘molecular glue’ to stabilize and promote the formation of a TIR1/AFB and Aux/IAA co-receptor complex. The formation of the SCF^{TIR1}-Aux/IAA co-receptor allows ubiquitylation of Aux/IAs, which are subsequently subjected to degradation through the 26S proteasome. Aux/

IAA degradation relieves ARF repression, allowing the ARFs to activate transcription (reviewed in [Morffy and Strader, 2022](#)).

The non-canonical TMK and extranuclear TIR1/AFB pathway

In addition to the SCF^{TIR1}-Aux/IAA nuclear auxin signaling pathway, TMK proteins also mediate transcription-independent cell surface auxin signaling (reviewed in [Ang and Ostergaard, 2023](#)). Moreover, the cytoplasmic-localized AFB1 activates auxin response independent of nuclear gene transcription ([Fendrych *et al.*, 2018](#); [Li *et al.*, 2021](#); [Serre *et al.*, 2021](#)). These non-canonical auxin signaling pathways are required for rapid auxin-induced response, but have not yet been implicated in the abiotic stress response.

Auxin roles in elevated temperature

Elevated temperatures causing heat stress affect plant growth and development, and globally result in the reduction of crop yields (reviewed in [Ding *et al.*, 2020](#)). A particular response to mildly elevated temperature is known as thermomorphogenesis (reviewed in [Casal and Balasubramanian, 2019](#)). The morphological changes include many auxin-related phenotypes such as elongated hypocotyls, increased petiole angle and length, and hyponastic growth (reviewed in [Casal and Balasubramanian, 2019](#)). When temperatures increase further, heat stress resistance mechanisms enable the plant to survive and grow under these conditions (reviewed in [Ding *et al.*, 2020](#)). Plants have evolved various efficient mechanisms for sensing and responding to high temperature, which involve the activation of phytohormone response and signal transduction (reviewed in [Casal and Balasubramanian, 2019](#)). Here, we review recent research progress of auxin guiding plant response to heat stress.

Auxin drives morphological changes that occur in response to elevated ambient temperature, known as thermomorphogenesis (reviewed in [Casal and Balasubramanian, 2019](#)). Increased auxin levels is a cornerstone of thermomorphogenesis. *PHYTOCHROME INTERACTING FACTOR 4 (PIF4)*, encoding a crucial thermomorphogenesis regulator, directly drives the expression of the auxin biosynthesis gene *YUC8* at 28 °C in Arabidopsis ([Sun *et al.*, 2012](#)). The *yuc8* mutant shows a decrease in hypocotyl elongation at higher temperatures in Arabidopsis, demonstrating the impact of auxin synthesis ([Sun *et al.*, 2012](#)). Additionally, transcript levels of auxin biosynthesis genes *TAA1* and *CYP79B* are diminished at higher temperatures in the *pif4* mutant ([Franklin *et al.*, 2011](#)), suggesting direct regulation of multiple auxin biosynthesis steps by heat.

Auxin transport also impacts thermomorphogenesis. The polar auxin inhibitor 1-naphthylphthalamic acid (NPA) inhibits thermal response at higher temperatures ([Stavang *et al.*, 2009](#)). Further, *PIN1* and *PIN2* reporter lines demonstrate decreased fluorescence at elevated temperatures ([Parveen and Rahman, 2021](#)). Further work will be required to determine

direct roles of regulating auxin transport in response to heat stress.

In addition to auxin biosynthesis and transport, auxin signaling is crucial for thermomorphogenesis. The auxin signaling mutants *tir1-1* ([Gray *et al.*, 1998](#)), *axr1-12* ([Gray *et al.*, 1998](#)), and *shy2-2/iaa3* ([Sun *et al.*, 2012](#)) display diminished hypocotyl elongation in response to elevated temperature. Furthermore, the stabilization of TIR1 at higher temperatures via HSP90 bolsters the auxin response ([Wang *et al.*, 2016](#)). The auxin-regulated family genes, *SMALL AUXIN UPREGULATED RNA (SAUR)*, have increased expression downstream of PIF4 at elevated temperatures ([Franklin *et al.*, 2011](#)). Together, these results demonstrate that not only the presence of cellular IAA, but also the ability to discern and respond to IAA is necessary for thermomorphogenesis.

Whereas thermomorphogenesis involves an increased auxin production and concomitant signaling, acute heat stress results in a disruption of auxin response and is responsible for agricultural disruption on a global scale ([Lobell and Field, 2007](#)). In particular, plants are vulnerable to heat stress during the development of pollen and male reproductive organs which is directly linked to diminished seed yield and quality (reviewed in [Chaturvedi *et al.*, 2021](#)). A growing body of literature demonstrates auxin biosynthesis, production, and transport guide anther and pollen development ([Cheng *et al.*, 2006](#); [Ru *et al.*, 2006](#); [Wu *et al.*, 2006](#); [Dal Bosco *et al.*, 2012](#); [Ding *et al.*, 2012](#); [Cecchetti *et al.*, 2015](#); [Yao *et al.*, 2018](#)). Critically, heat stress disrupts auxin processes in crop species and is likely to be a contributing factor to diminished pollen viability. In maize, it is estimated that every day with temperatures >30 °C results in a 1% loss in yield ([Lobell and Field, 2007](#); [Lobell *et al.*, 2011](#)). Thus, understanding the interplay of auxin and heat stress across agricultural plants is a challenge and an opportunity for agricultural advancement in the face of a changing global climate.

Auxin biosynthesis is critical to pollen formation at multiple stages. For example, the Arabidopsis *yuc2 yuc6* auxin biosynthesis mutant fails to produce viable pollen due to arrested development early during gametogenesis ([Cheng *et al.*, 2006](#); [Yao *et al.*, 2018](#)). Auxin biosynthesis is also important during the production of male reproductive structures in crop species and is disrupted at high temperatures. During heat stress, endogenous auxin levels and transcript levels of auxin biosynthesis genes are decreased in Arabidopsis, barley anthers, and rice spikelets, suggesting negative effects of warm temperatures on auxin levels ([Sakata *et al.*, 2010](#); [Du *et al.*, 2013a](#); [Min *et al.*, 2014](#); [Wu *et al.*, 2016](#); [Sharma *et al.*, 2018](#)). Decreased auxin levels correspond to decreased transcript accumulation of auxin biosynthesis genes *YUC6*, *YUC8*, and *TAA1* ([Sakata *et al.*, 2010](#); [Sharma *et al.*, 2018](#)). Interestingly, the application of exogenous auxin during heat stress has been found to mitigate damaging impacts of heat shock on pollen viability, sterility, and overall grain yield in multiple crop species including wheat, rice, and barley ([Sakata *et al.*, 2010](#); [Sharma *et al.*, 2018](#);

Abeyasingha *et al.*, 2021). Together, these results suggest that the availability of free IAA plays an important role in mitigating heat stress during pollination.

Auxin signaling also guides pollen development and is differentially regulated during heat stress. In Arabidopsis, *arf17* knockout mutants display male sterility, have decreased *DR5* signal within the anthers, and have disrupted callose deposition surrounding pollen tetrads (Yang *et al.*, 2013). Further, *arf6 arf8* double mutants are sterile and contain indehiscent anthers (Nagpal *et al.*, 2005; Ru *et al.*, 2006; Wu *et al.*, 2006). Interestingly, *ARF13/ARF17* and *ARF6/ARF8* are regulated by *miRNA160* and *miR167*, respectively (Wu *et al.*, 2006). *ARF* regulation by miRNAs in response to heat stress translates to crop species, including barley and cotton (Kruszka *et al.*, 2014). In cotton (*Gossypium hirsutum*), comparative studies between heat-insensitive strain 84021 and heat-sensitive H05 demonstrated that decreased *miR160* levels and concomitant increased levels of its target *ARF17* are found in the heat-insensitive strain 84021 compared with the heat-sensitive strain H05 (Ding *et al.*, 2017). Further, overexpressing *miRNA160* in the heat-insensitive 84021 resulted in anther indehiscence resembling the heat-sensitive strain H05. In contrast to rice and barley, exogenous application of auxin to cotton exacerbated the impacts of long-term heat stress on sterility. Further studies should explore the impacts of exogenous auxin across multiple species to understand the described opposing roles for auxin in this process. Further, it appears that the role of miRNA regulation in response to heat stress appears to be conserved in plants and could provide a potential area of research for agricultural advancement (Wu *et al.*, 2006; Kruszka *et al.*, 2014; J. Zhao *et al.*, 2016; Ding *et al.*, 2017).

Auxin further regulates anther development in Arabidopsis (Cecchetti *et al.*, 2008). The auxin transporters PIN5 and PIN8 are present in the endoplasmic reticulum of developing pollen grain (Dal Bosco *et al.*, 2012; Ding *et al.*, 2012); these two PINs act antagonistically, as the *pin5pin8* double mutant rescues the aberrant pollen morphology found in each of the single mutants. Pollen viability in the double mutant also suggests that additional auxin transporters regulate this process (Ding *et al.*, 2012). Other auxin efflux carriers, ABCB1 and ABCB19, also impact stamen development (Cecchetti *et al.*, 2008). ABCB1 plays a major role in anther development; *abcb1* mutants display anther indehiscence and defective pollen development. Whereas auxin guides anther development, little is known about the impact of temperature stress on auxin transport genes. While these auxin transporters impact male sterility, their intersection with heat stress warrants further exploration. Other transporters such as the phosphate transporter OsPT8 bolster thermotolerance through changes in auxin distribution in *Nicotiana tabacum* (Z. Song *et al.*, 2019). These changes in thermotolerance are conferred along with increased transcript levels of *YUC* auxin biosynthesis genes, *PIN1* and *PIN2* auxin transport genes, and *ARF1* and *ARF2* auxin signaling genes (Z. Song *et al.*, 2019). Transcriptome data from heat-resistant

cultivars of cotton and rice (Min *et al.*, 2014; Sharma *et al.*, 2021) also reveal a correlation between heat stress changes in auxin transport and signal components and tolerance to heat stress. Whereas auxin transport is probably impacted at higher temperatures, more work should be done to target auxin transport genes involved in male sterility at higher temperatures.

Taken together, auxin biosynthesis, transport, and signaling guide plants' response to heat stress (Table 1). Interestingly, the role of auxin at elevated temperatures appears to have two distinct effects. At mildly elevated temperatures, auxin synthesis and signaling increase to drive thermomorphogenesis. However, once past a critical temperature threshold, heat stress results in aberrant auxin signaling which threatens global food supplies by impacting pollen development (Lobell *et al.*, 2011). Moving forward, it will be critical to understand which temperatures (and for what durations) impact pollen viability among agriculturally important crops. Additionally, the impact of exogenous auxin treatment to mitigate the impacts of heat stress needs to be better understood. Whereas exogenous auxin treatment of barley anther and spikelets improves yield, similar treatments hinder pollen viability in cotton. Further comparisons should be made to understand differences in development and phytohormone crosstalk which might reconcile these differences.

Auxin roles in salinity stress

Worldwide, soil salinity has increased dramatically in recent years, with a major impact on global ecosystems and agricultural production (reviewed in Zandalinas *et al.*, 2021). In particular, temperature extremes have become more frequent and intense, resulting in the lack of sufficient water and salt accumulation in the soil (reviewed in Gamalero and Glick, 2022). The salinity-related cations Na^+ , Mg^{2+} , and Ca^{2+} , and the anions SO_4^{2-} , Cl^- , and HCO_3^- have deleterious effects on plant growth when in excess. Amongst these constituents, NaCl represents 50–80% of the total soluble salts in the soil (Joshi *et al.*, 2022). Salt stress affects plants throughout their life cycle, from inhibiting seed germination to modulating plant growth and development at all stages. When plants are first exposed to high levels of salt, a decrease of plant growth rate occurs. Subsequently, following the continued uptake of salt, sodium ions are translocated and accumulated in plants, resulting in the generation of a number of reactive oxygen species (ROS), which in turn negatively affect the plant yield and quality (reviewed in Gamalero and Glick, 2022). There are three major effects of salt on plants: water deficit, ion toxicity, and ion imbalance. Plants use a range of mechanisms to deal with salt stress, including exclusion of sodium ions, modulation of root uptake and transport, synthesis of various antioxidative enzymes, and modulation of some plant hormone levels (reviewed in Gamalero and Glick, 2022). Amongst these plant hormones, auxin has been reported to play essential roles during exposure to high salinity.

Auxin biosynthesis and transport are regulated in response to salt stress in plants. Overexpression of auxin biosynthesis genes leads to increased salt tolerance in multiple species (Dunlap and Binzel, 1996; Kim *et al.*, 2013; Ke *et al.*, 2015; Yan *et al.*, 2016). For example, the expression of auxin biosynthesis genes *NIT1*, *NIT2*, and *YUC4* is significantly increased in response to NaCl treatment in Arabidopsis (Cackett *et al.*, 2022). The *YUC* family of auxin biosynthesis genes are induced under salt stress in *Cucumis sativus* and potato (Kim *et al.*, 2013; Yan *et al.*, 2016). IAOx pathway genes *CYP79B2* and *CYP79B3* show induction under mild salt stress (Julkowska *et al.*, 2017). In the moss *Physcomitrium patens*, loss of the auxin-conjugating GH3 enzymes results in tolerance to high salt concentrations (Koochak and Ludwig-Muller, 2021). These results suggest a connection between auxin biosynthesis and salt stress response. Further, auxin transport is impaired under salt stress (Ribba *et al.*, 2020). *PIN1*, *PIN3*, and *PIN7* expression is negatively regulated under salt stress, which impacts PIN protein abundance and consequently inhibits auxin transport (Liu *et al.*, 2015; Fu *et al.*, 2019). Expression of *CcPIN* genes is regulated by salt treatment in Chinese hickory (Yang *et al.*, 2022). *PIN1* plays a critical role in regulating plant epidermal cell development under salt and drought stress (Bawa *et al.*, 2022). Moreover, *PIN2* and *AUX1* display altered subcellular localization under salt stress. *PIN2* phosphorylation status changes via the activity of PINOID (PID) under salt stress (Wang *et al.*, 2019). *LAX3* transcript levels are induced by overexpression of *WRKY3*, which results in salt stress tolerance (Hichri *et al.*, 2017). Finally, auxin transporters are crucial for producing the asymmetric distribution of auxin to drive bending away from salt in the growth substrate (Galvan-Ampudia *et al.*, 2013; van den Berg *et al.*, 2016), providing a means to escape salt stress by root systems. These clues point towards a role for auxin levels and distribution in salt stress response.

In addition to auxin biosynthesis and transport, auxin signal transduction is also involved in salt stress response. The *tir1/afb2/afb3* mutants, defective in multiple TIR/AFB receptors, display hypersensitivity to NaCl treatment in the root meristem, suggesting that the slowing of root growth might be an adaptive mechanism for plants surviving under a salt environment (Iglesias *et al.*, 2010; Yu *et al.*, 2020). Contrasting data suggest that *TIR1* and *AFB2* are down-regulated by salt stress, indicating that decreasing auxin response may be involved in plant growth and adaptation to salt (Iglesias *et al.*, 2014; Yu *et al.*, 2020). Moreover, overexpression of the auxin receptor gene *AFB3* (*AUXIN F-BOX3*) results in an increased resistance to salinity in Arabidopsis roots (Garrido-Vargas *et al.*, 2020). Overexpression of *MdIAA8*, *MdIAA9*, and *MdIAA25* in transgenic apple calli results in salt stress tolerance (Y. Li *et al.*, 2022). Although there is limited information on the role of Aux/IAAs in response to salt stress, *IAA17* is stabilized by the application of exogenous nitric oxide and is also accumulated under salt stress, suggesting the important role of *IAA17* in stress signaling (Liu *et al.*, 2015; Shi *et al.*, 2017; Jing *et al.*, 2023).

In contrast to Aux/IAA proteins, ARF proteins have been characterized as important components to salt stress responses (Ribba *et al.*, 2020). For example, salt response *cis*-elements in the *ARF* gene promoters along with the response elements for MYB and MYC, transcription factors involved in stress response, suggest direct transcriptional regulation (Bouzroud *et al.*, 2018). In rice, *OsARF11* and *OsARF15* genes are differentially expressed under salt conditions (Jain and Khurana, 2009). Overexpression of sweet potato *IbMP/ARF5* leads to an enhanced salt and drought tolerance in Arabidopsis (Kang *et al.*, 2018). Several *ARF* transcripts are post-transcriptionally regulated by miRNAs during salt stress, suggesting a crucial role for ARF proteins in the integration of environmental signals (Kinoshita *et al.*, 2012; Kang *et al.*, 2018). The expression of *ARF3.1*, *ARF3.2*, and *ARF4* is significantly inhibited by salt treatment in *Populus* spp. (He *et al.*, 2018). Thus, multiple auxin signaling components alter salt stress response across species.

Taken together, auxin is important in response to salt stress (Table 1), modulating a complex balance of biosynthesis, transport, and signal transduction, tuning physiological changes in plant architecture and salt stress adaptation.

Auxin roles in drought stress

As a major abiotic environmental stress, drought is related to water scarcity and access. Drought stress causes multiple physiological, metabolic, and biochemical changes that limit plant growth and thus reduce crop yields. To survive and maintain growth, plants adjust their morphological and physiological characteristics in response to drought. One strategy is to maintain physiological water balance through increasing water uptake via roots, reducing water loss by closing stomata, and adjusting osmotic potential within tissues (reviewed in Gupta *et al.*, 2020). Many phytohormones play roles in drought stress tolerance (reviewed in Kim *et al.*, 2022), with abscisic acid (ABA) being ascribed the largest and best described role. Here, we focus on the role of auxin in drought stress (Table 1), with its interaction with ABA highlighted.

Auxin biosynthesis and transport are implicated in drought stress response. Increasing auxin levels in different species by either overexpression of *YUC* family genes or application of auxin enhances drought resistance. In particular, overexpression of *YUC6* and *YUC7* enhances drought resistance in different species (Lee *et al.*, 2012; Kim *et al.*, 2013; Park *et al.*, 2019). Similarly, *yuc1yuc2yuc6* triple mutants with a lower IAA level show decreased drought resistance (Shi *et al.*, 2014). Increasing endogenous auxin levels by overexpression of bacterial tryptophan-2-monooxygenase (*iaaM*) enhances drought tolerance, whereas auxin application increases ROS detoxification and the expression of ABA-related stress genes *RAB18*, *RD22*, *RD29A*, *RD29B*, *DREB2A*, and *DREB2B* in Arabidopsis, linking ABA and auxin in growth-stress trade-offs (Shi *et al.*, 2014). In white clover, application of IAA during stress increased relative water

Table 1. Plant genes of auxin metabolism, transport, and signaling involved in abiotic stress

Heat stress		Salt stress	
Gene	Reference	Gene	Reference
TAA1	Franklin <i>et al.</i> (2011); Sharma <i>et al.</i> (2018)	NIT1	Cackett <i>et al.</i> (2022)
CYP79B	Franklin <i>et al.</i> (2011)	NIT2	Cackett <i>et al.</i> (2022)
YUC6	Sharma <i>et al.</i> (2018)	YUC4	Cackett <i>et al.</i> (2022)
YUC8	Sun <i>et al.</i> (2012)	YUC	Kim <i>et al.</i> (2013); Yan <i>et al.</i> (2016)
NPA	Stavang <i>et al.</i> (2009)	CYP79B2	Julkowska <i>et al.</i> (2017)
PIN1	Parveen and Rahman (2021)	CYP79B3	Julkowska <i>et al.</i> (2017)
PIN2	Parveen and Rahman (2021)	PIN1	Liu <i>et al.</i> (2015); Fu <i>et al.</i> (2019)
TIR1	Gray <i>et al.</i> (1998)	PIN2	Wang <i>et al.</i> (2019)
AXR1	Gray <i>et al.</i> (1998)	PIN3	Liu <i>et al.</i> (2015); Fu <i>et al.</i> (2019)
IAA3	Sun <i>et al.</i> (2012)	PIN7	Liu <i>et al.</i> (2015); Fu <i>et al.</i> (2019)
ARF1	Z. Song <i>et al.</i> (2019)	AUX1	Wang <i>et al.</i> (2019)
ARF2	Z. Song <i>et al.</i> (2019)	LAX3	Hichri <i>et al.</i> (2017)
ARF6	Wu <i>et al.</i> (2006); Kruszka <i>et al.</i> (2014)	GH3	Mellor <i>et al.</i> (2016); Koochak and Ludwig-Muller (2021)
ARF8	Wu <i>et al.</i> (2006); Kruszka <i>et al.</i> (2014)	TIR1	Iglesias <i>et al.</i> (2010); Yu <i>et al.</i> (2020)
ARF13	Wu <i>et al.</i> (2006); Kruszka <i>et al.</i> (2014)	AFB2	Iglesias <i>et al.</i> (2010); Yu <i>et al.</i> (2020)
ARF17	Wu <i>et al.</i> (2006); Yang <i>et al.</i> (2013); Kruszka <i>et al.</i> (2014); Ding <i>et al.</i> (2017)	AFB3	Iglesias <i>et al.</i> (2010); Garrido-Vargas <i>et al.</i> (2020); Yu <i>et al.</i> (2020)
Drought stress		IAA17	Liu <i>et al.</i> (2015); Shi <i>et al.</i> (2017)
Gene	Reference	MdIAA8	Y. Li <i>et al.</i> (2022)
YUC1	Shi <i>et al.</i> (2014)	MdIAA9	Y. Li <i>et al.</i> (2022)
YUC2	Shi <i>et al.</i> (2014)	MdIAA25	Y. Li <i>et al.</i> (2022)
YUC6	Kim <i>et al.</i> (2013); Shi <i>et al.</i> (2014)	OsARF11	Jain and Khurana (2009)
YUC7	Lee <i>et al.</i> (2012); Park <i>et al.</i> (2019)	OsIAA15	Jain and Khurana (2009)
iaaM	Shi <i>et al.</i> (2014)	IbMp/ARF5	Kang <i>et al.</i> (2018)
OsPIN2	Du <i>et al.</i> (2013b)	ARFs	Kinoshita <i>et al.</i> (2012); Kang <i>et al.</i> (2018); Ribba <i>et al.</i> (2020)
OsPIN3t	Zhang <i>et al.</i> (2012)	ARF3.1	He <i>et al.</i> (2018)
OsPIN5b	Du <i>et al.</i> (2013b)	ARF3.2	He <i>et al.</i> (2018)
GmLAXs	Yang <i>et al.</i> (2021)	ARF4	He <i>et al.</i> (2018)
IAA5	Salehin <i>et al.</i> (2019)	Cold stress	
IAA6	Salehin <i>et al.</i> (2019)	Gene	Reference
IAA19	Salehin <i>et al.</i> (2019)	YUC	Du <i>et al.</i> (2013b)
OsIAA18	Wang <i>et al.</i> (2021); A. Zhang <i>et al.</i> (2021)	OsGH3	Du <i>et al.</i> (2013b)
OsIAA20	Wang <i>et al.</i> (2021); A. Zhang <i>et al.</i> (2021)	SgGH3.1	Jiang <i>et al.</i> (2021)
TAIAA15-1A	Jain and Khurana (2009)	PIN2	Shibasaki <i>et al.</i> (2009); Ashraf and Rahman (2019)
SIARFs	Bouzroud <i>et al.</i> (2018)	PIN2	Shibasaki <i>et al.</i> (2009); Ashraf and Rahman (2019)
SIARF4	Bouzroud <i>et al.</i> (2020); Chen <i>et al.</i> (2021)	PIN3	Shibasaki <i>et al.</i> (2009)
BdARFs	S. Song <i>et al.</i> (2019)	IAA14	Aslam <i>et al.</i> (2020)
SbARFs	Wang <i>et al.</i> (2007)	CsARF5	X. Zhang <i>et al.</i> (2021)
OsARFs	Wang <i>et al.</i> (2007)	ARFs	Hannah <i>et al.</i> (2005); Jain and Khurana (2009)
GmARFs	Ha <i>et al.</i> (2013)	Aux/IAA	Hannah <i>et al.</i> (2005); Jain and Khurana (2009)
IbARF5	Kang <i>et al.</i> (2018)		
AcARFs	Su <i>et al.</i> (2021)		

and total chlorophyll content under drought conditions while also increasing ABA and jasmonic acid (JA) abundance (Zhang *et al.*, 2020). PIN proteins OsPIN2 and OsPIN5b are up-regulated by drought stress in rice (Du *et al.*, 2013a). In another example, overexpression of *OsPIN3t* improved survival rates under approximated drought conditions created with 20% polyethylene glycol (PEG) (Zhang *et al.*, 2012). Further, *GmLAX* genes which are up-regulated during PEG and ABA treatment are thus thought to be involved in drought response in soybean (Yang *et al.*, 2021). Each of these examples points to a role for auxin levels and distribution in drought tolerance across several species.

Auxin signaling components are also affected by drought response and play roles in stress tolerance. Recent studies have identified that many Aux/IAA proteins may act as a hub that integrates other pathways including ABA. Loss-of-function mutants of *IAA5*, *IAA6*, and *IAA19* display decreased drought tolerance in Arabidopsis; these *Aux/IAA* genes are directly targeted by the stress factor DREB/CBF proteins (Salehin *et al.*, 2019). Overexpression of *OsIAA18* and *OsIAA20* enhances rice tolerance against drought stress (Wang *et al.*, 2021; A. Zhang *et al.*, 2021). The wheat *Aux/IAA* gene *TaIAA15-1A* enhances plant tolerance against drought stress by regulating ABA-related genes (Su *et al.*, 2023). SAUR proteins such as SAUR32 has also been implicated in ABA-mediated stomatal closure during drought stress (He *et al.*, 2021).

The ARFs are also regulated by drought stress in both Arabidopsis and crop species such as tomato. Many tomato *SLARF* genes, including *SLARF1*, *SLARF2A*, *SLARF2B*, *SLARF4*, *SLARF6A*, *SLARF6B*, *SLARF8A*, *SLARF9A* and *SLARF18*, are induced under drought stress in tomato (Bouzroud *et al.*, 2018). Interestingly *ARF7A* is repressed by stress in the shoot but induced by stress in the root (Bouzroud *et al.*, 2018). Loss of *SLARF4* activity by either artificial miRNA knockdown or Cas9 editing increases drought and salinity tolerance (Bouzroud *et al.*, 2020; Chen *et al.*, 2021). *BdARF4* (*Brachypodium distachyon*), along with *BdARF8* and *BdARF17*, are up-regulated during drought stress (S. Song *et al.*, 2019). *SbARF10*, *16*, and *21* are up-regulated in *Sorghum bicolor* (Wang *et al.*, 2010). In rice, *OsARF2*, *OsARF4*, *OsARF10*, *OsARF14*, *OsARF16*, *OsARF18*, *OsARF19*, *OsARF22*, and *OsARF23* are induced in leaves and roots exposed to drought (Wang *et al.*, 2007). In soybean (*Glycine max*), nearly all ARF genes are induced by water deficit (Ha *et al.*, 2013). Expressing *IbARF5* (*Ipomoea batatas*) in Arabidopsis improves drought tolerance, probably by inducing ABA biosynthesis (Kang *et al.*, 2018). In *Actinidia chinensis* (kiwifruit), *AcARF1a*, *19a*, *26a*, *28a*, *28b*, *5*, and *7* are up-regulated after drought (Su *et al.*, 2021). These results implicate ARF proteins in drought stress, in particular *SLARF4* and *IbARF5* as mutants of or overexpression of these genes can increase drought tolerance (Kang *et al.*, 2018; Bouzroud *et al.*, 2020; Chen *et al.*, 2021).

In most cases, changes in auxin levels or signaling activation affect drought tolerance through reduced ROS production and/or increasing ABA levels (Shi *et al.*, 2014; Park *et al.*,

2019; Wang *et al.*, 2021; A. Zhang *et al.*, 2021; Su *et al.*, 2023). This connection is not surprising, as there are many points of auxin–ABA crosstalk in growth and development (Emenecker and Strader, 2020). A better understanding of auxin and ABA interactions in drought stress would yield insight into coordination of growth and stress response.

Much of the work connecting auxin to drought stress response has been done in crop species. Detailed molecular analysis of auxin components that are altered during drought stress is needed to better understand auxin's role in drought tolerance and to possibly provide tools to enhance drought tolerance. For example, for the ARF and Aux/IAAs, only down-regulation of *SLARF4* and overexpression of *IbARF5* in Arabidopsis have been shown to alter drought tolerance in addition to reducing *TaIAA15-1A* in wheat. The overexpression of *AtYUC6* in potato increases drought tolerance, but reduced tuber yield, highlighting the difficulty in optimizing growth–stress trade-offs in crop species by modulating the auxin pathway (Kim *et al.*, 2013).

Auxin roles in cold stress

Cold stress deleteriously impacts plant survival, growth, and productivity, and limits geographical distribution of various plant species (reviewed in Kidokoro *et al.*, 2022). Plants are frequently exposed to cold stress, including both chilling (0–12 °C) and freezing (<0 °C) stresses (reviewed in Ding *et al.*, 2020). Chilling temperatures inhibit plant growth, but freezing temperatures destroy cell membranes, leading to cell death (reviewed in Kidokoro *et al.*, 2022). Plants have evolved diverse systems to adapt and survive under low temperatures, referred to as cold acclimation. Cold sensors such as calcium channels and CHILLING TOLERANCE DIVERGENCE 1 (COLD1) perceive cold temperature (Ma *et al.*, 2015; Zhang *et al.*, 2019) whereas the C-repeat-binding factor (CBF)/dehydration-responsive element-binding factor (DREB1) activates cold-responsive (COR) genes for plant response to cold stress (Novillo *et al.*, 2007; Jia *et al.*, 2016; C. Zhao *et al.*, 2016). Current studies indicate that CBF-dependent signaling pathways play a prominent role in cold stress (Shi *et al.*, 2018). Additionally, many physiological and sophisticated molecular mechanisms exist during cold acclimation, including auxin response and its regulation.

Cold stress affects auxin levels differently depending on plant species, developmental stage, and physiological settings (Fukaki and Tasaka, 1999; Wyatt *et al.*, 2002; Kosova *et al.*, 2012; Majlath *et al.*, 2012; Maruyama *et al.*, 2014). Cold stress inhibits the gravitropic growth of stems and roots in Arabidopsis and rice (Fukaki and Tasaka, 1999; Wyatt *et al.*, 2002). Application of auxin analogs induces the accumulation of freeze-protective metabolites and soluble sugars during cold stress in *Brassica napus* (Gaveliene *et al.*, 2013). Auxin levels increase under low temperatures in wheat (*Triticum aestivum* L.) (Wang *et al.*, 2023).

Many auxin-related genes are significantly affected under cold stress in Arabidopsis and rice, including auxin efflux carrier genes, ARF transcription factor genes, and transcription repressor *Aux/IAA* genes (Hannah *et al.*, 2005; Jain and Khurana, 2009). Moreover, cold treatment increases the expression of the *YUC* family members and reduces that of the *OsGH3* family gene in rice (Du *et al.*, 2013a). Overexpression of *SgGH3.1* alters the sensitivity to exogenous IAA, induces *AtCBF1–AtCBF3* gene expression, and enhances the chilling tolerances in Arabidopsis (Jiang *et al.*, 2021). Cold stress inhibits root elongation and gravity response by inhibiting the intracellular trafficking of auxin efflux carriers PIN2 and PIN3 (Shibasaki *et al.*, 2009). Further studies indicate that cold stress affects the polar transport of auxin by modulating intracellular cycling of PIN2 (Ashraf and Rahman, 2019). Moreover, mutants defective in the auxin transcriptional repressor *IAA14* display a hypersensitive response under cold stress in Arabidopsis (Aslam *et al.*, 2020). Overexpression of the auxin transcription factor gene *CsARF5* enhances the chilling tolerance in cucumber, suggesting an important role in cold stress (X. Zhang *et al.*, 2021).

Taken together, these findings suggest a link between cold stress and auxin response in regulation of plant growth and development (Table 1). However, compared with our understanding of auxin roles under elevated temperatures, auxin roles under cold stress are not well understood.

Conclusion and perspectives

Plants grown in the natural environment are subjected to a range of abiotic stresses, which affect plant growth and development. Abiotic stress factors that are particularly detrimental to plants include extremes of temperature, drought, and high salinity. To survive and maintain growth, plants have evolved diverse systems at the molecular, cellular, and physiological levels for adapting and surviving under adverse growth conditions. The phytohormone auxin plays critical roles in regulation of abiotic stresses (Table 1), although these roles are better defined for some stresses than for others.

Altering auxin levels, either through its application or by overexpressing auxin biosynthesis genes, can mitigate the impact of drought, heat, salinity, and cold stress, but mechanistic insight into how this occurs is largely lacking. This connection between auxin and stress tolerance, while not fully elucidated, provides a potential research direction for improving stress tolerance in agricultural settings. For example, defects in *SLARF4* result in increased drought and salinity tolerance (Bouzroud *et al.*, 2020; Chen *et al.*, 2021), a feature that could be leveraged in tomato, and perhaps other crops, to engineer resilience. Additionally, a better understanding of auxin and other hormone crosstalk interactions may provide tools for crop improvement. Many points of interaction between auxin and ABA, and JA have been

uncovered (Emenecker and Strader, 2020). Understanding how these known interactions regulate growth during stress would provide more mechanistic insight into auxin's role in abiotic stress.

Further, insights into auxin and stress-protective metabolites may prove fruitful in increasing stress tolerance in crop species. Glucosinolates (GLSs) are secondary metabolites found in *Brassicaceae* that are involved in resilience to herbivore and pathogen attack and have also been found to regulate growth (Katz *et al.*, 2015). The loss of *Aux/IAA* 5, 6, and 9 decreases GLS content during drought stress and leads to a defect in stomatal regulation (Salehin *et al.*, 2019). Glucosinolates are but one example of downstream molecules activated by auxin to buffer resilience in response to stress, and more studies are needed to fully uncover connections between auxin, secondary metabolites, and stress response. Additional potential agricultural applications for auxin in abiotic stress response include the following:

- Identification of downstream auxin factors which bolster stress responses in stress-tolerant cultivars using multi-omic studies between established stress-resistant and -sensitive crop varieties could identify new targets for breeding (Sharma *et al.*, 2021; Da Ros *et al.*, 2023).
- Validation of stress-related secondary metabolites which are activated by auxin-related stress responses in crop species to identify effectors of auxin effects on stress response. For example, auxin signaling drives the expression of freeze-protective metabolites in cold stress (Gaveliene *et al.*, 2013), and downstream application of exogenous GLSs facilitates the response to drought stress.
- Using nuanced ways such as synthetic biology to alter auxin biosynthesis, signaling, and transport during developmental stages when plants are vulnerable to abiotic stress (i.e. pollen development and seedling establishment) could be a tool to regulate plant growth during stressful conditions (Brophy, 2022).
- Modulation of miRNAs (i.e. MiR160 and 167) to alter ARF abundance during abiotic stress (Wu *et al.*, 2006; Kruszka *et al.*, 2014; Ding *et al.*, 2017) could be used in crop species to engineer stress resilience.
- Integration of new technologies such as CRISPR to edit auxin-related genes in crop species (Chen *et al.*, 2021) and/or use of single-cell and tissue-specific approaches to identify and modify processes regulating abiotic stress response in vulnerable tissues of crop species (Mesihovic *et al.*, 2016; Nelms and Walbot, 2019; Chaturvedi *et al.*, 2021; X. Li *et al.*, 2022).

The study of auxin modulation under abiotic stresses is growing. However, it is crucial to understand the mechanisms of auxin involved not only under single stress conditions, but also under multiple stresses. Many gaps remain in our understanding of auxin in responses to abiotic stress, particularly in stress sensing, early signaling, and post-translational regulation.

Thus, more work is needed to explore the role of auxin in abiotic stress, providing detailed mechanisms for improving crop productivity and agricultural applications.

Author contributions

HJ, EGW, KSE, and LCS wrote the manuscript.

Conflict of interest

LCS is on the Science Advisory Board for Prose Foods.

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