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Role of transcriptional regulation in auxin-mediated response to abiotic stresses

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Global climate change (GCC) is posing a serious threat to organisms, particularly plants, which are sessile. Drought, salinity, and the accumulation of heavy metals alter soil composition and have detrimental effects on crops and wild plants. The hormone auxin plays a pivotal role in the response to stress conditions through the fine regulation of plant growth. Hence, rapid, tight, and coordinated regulation of its concentration is achieved by auxin modulation at multiple levels. Beyond the structural enzymes involved in auxin biosynthesis, transport, and signal transduction, transcription factors (TFs) can finely and rapidly drive auxin response in specific tissues. Auxin Response Factors (ARFs) such as the ARF4, 7, 8, 19 and many other TF families, such as WRKY and MADS, have been identified to play a role in modulating various auxin-mediated responses in recent times. Here, we review the most relevant and recent literature on TFs associated with the regulation of the biosynthetic, transport, and signalling auxin pathways and miRNA-related feedback loops in response to major abiotic stresses. Knowledge of the specific role of TFs may be of utmost importance in counteracting the effects of GCC on future agriculture and may pave the way for increased plant resilience.

KEYWORDS

global climate change, stress tolerance, transcription factor, auxin, drought stress, salt stress, heavy metals

1 Introduction

Global climate change (GCC) is producing significant environmental disruptions with potentially damaging consequences for the persistence of all life forms across biomes (Bernatchez et al., 2023). The direct consequences of GCC include, among others, extreme temperature waves and water scarcity, which lead to increased soil salinity, and the increase of nonessential elements, among them heavy metals (HMs), thereby increasing the risk of environmental contamination. These abiotic stressors can negatively impact the growth and productivity of plants, functioning below optimal levels (Cramer et al., 2011), which leads to substantial losses in the agricultural economy. Plants cope with these stressful and unfavourable factors by evolving their ability to survive wide-ranging abiotic stresses.

To this end, plants have developed elaborate regulatory mechanisms that enable them to withstand adverse growth conditions through biochemical routes that control how plants respond. These pathways include stress detection, signal transmission, and adjustments in physiological parameters to attain varying levels of tolerance (Zhang et al., 2022). Notably, among these factors, several plant hormones facilitate adaptation to abiotic stresses. In this regard, it has been shown that auxin, one of the main phytohormones, regulates plant growth in response to abiotic stresses, such as drought and salinity, influencing root cell activity or differentiation, depending on its different distribution in this organ (Sabatini et al., 1999; Blilou et al., 2005; Dello Ioio et al., 2008; Di Mambro et al., 2017; Kalve et al., 2020; Ghelli et al., 2023). The accumulation of this phytohormone in tissues is mainly modulated by its biosynthetic, signalling, and transport routes. These pathways can be regulated at multiple levels, such as epigenetic, transcriptional, and post-translational (Terrile et al., 2012; Van Der Woude et al., 2019; Marzi et al., 2020; Powers and Strader, 2020). Controlling gene expression is one of the most investigated mechanisms in plants for rapidly and finely adapting transcriptional programmes in response to changes in the environment. Transcription factors (TFs) are proteins that bind to DNA and specifically target cis-acting elements in the promoter region of eukaryotic genes to control their expression (Lelli et al., 2012; Lambert et al., 2018). Previous research on TFs related to auxin homeostasis has highlighted the central role of the antagonistic interaction between auxin response factors (ARFs), most of which are auxin signalling enhancers, and Auxin/INDOLE-3-ACETIC ACID (AUX/IAAs), a large family of auxin co-receptors and transcriptional repressors. Both Aux/IAA and ARFs were shown to play a pivotal role in bridging auxin signalling to that of other phytohormones, such as abscisic acid (ABA). The interaction between auxin and ABA is a key part of fine-tuning of plants responses to abiotic stress. It helps plants deal with drought in a number of ways, such as by closing their stomata to stop water loss (Salehin et al., 2019) or by controlling proline biosynthesis, an amino acid having a highly beneficial role in stress response (Hayat et al., 2012; Zhang et al., 2021). Severe environmental conditions such as drought, salinity, or HM accumulation prompt an oxidative burst through the rise of reactive oxygen species (ROS). These are a group of very reactive molecules that include the superoxide anion ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($^{\cdot}OH$), and singlet oxygen ($^1O_2$). At low levels, these compounds function as signalling components, regulating important metabolic pathways, whereas when their levels increase beyond a 'safe threshold', they can be responsible for oxidative damage (Hasanuzzaman et al., 2020; Puglia, 2023). This leads to a number of harmful effects, such as lipid peroxidation, increased membrane permeability, disruption of the antioxidant system, induction of mitochondrial degradation, and DNA and RNA damage (Kurek et al., 2019; Hasanuzzaman et al., 2020). Thus, the regulation of ROS homeostasis is of primary importance in the tolerance to abiotic stresses, and it is achieved by the antioxidative defence systems, including enzymatic and non-enzymatic responses (Hasanuzzaman et al., 2020; Puglia, 2023).

In this study, we present an updated overview aimed at unveiling the importance of auxin regulation in response to abiotic stresses attained through transcriptional regulation of its biosynthetic, signalling, and transport pathways. We will take into consideration novel findings on *Arabidopsis thaliana* model species as well as translational studies on crop species such as tomato and rice. Moreover, in this review, we highlight promising players recently discovered that can provide new tools for the enhancement of plant tolerance to GCC-enhanced abiotic stress effects.

2 Auxin biosynthesis, transport, and signalling

The biosynthesis of indole-3-acetic acid (IAA), the main natural auxin, occurs via two pathways, one dependent on tryptophan (Trp) and another Trp independent (Cao et al., 2019; Sato et al., 2022). Tryptophan is produced from chorismate through the intermediate indole-3-glycerol phosphate (IGP), with the anthranilate synthase alpha subunit (ASA) serving as the initial enzyme in the tryptophan synthesis process. Downstream of Trp production, in the indole-3-acetaldoxime (IAOx) pathway, indole-3-acetonitrile (IAN) is converted to IAA via nitrilase (NIT) (Zhao, 2010). While in the TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS/YUCCA (TAA/YUC) pathway, the structural enzyme tryptophan aminotransferase (TAA1), through an amino-transfer reaction, converts Trp to indole-3-pyruvic acid (IPyA), which is then decarboxylated to form IAA by flavin-containing monooxygenases (FMOs) of the YUCCA (YUC) type (Figure 1). Recent studies have shown that the reversible TAA1 reaction, which prevents over- or under-accumulation of IPyA based on different Km values of Trp and IPyA, finely regulates this two-step biosynthetic pathway (Sato et al., 2022). This mechanism allows the concentration of IPyA to be kept low so that it can only be converted enzymatically to IAA by the irreversible and rate-limiting reaction catalysed by YUC, avoiding the non-enzymatic generation of IAA (Cao et al., 2019; Sato et al., 2022).

The uneven distribution of auxin level is attained by the directional auxin transport mediated by specific families of influx, AUXIN RESISTANT1/LIKE AUX1 (Aux/LAX) (Swarup and Bhosale, 2019), or efflux channel proteins, PIN-FORMED (PIN) (Křeček et al., 2009; Nodzyński et al., 2016) (Figure 1). The precise positioning of these auxin channels orients auxin flux and creates heterogeneity for IAA distribution. PIN protein activity can be regulated at many levels, including regulation of transcription, protein degradation, subcellular trafficking (endocytic recycling and polarised targeting), and transport activity (Křeček et al., 2009; Kumar et al., 2024).

Auxin, as a signalling molecule, plays an instrumental role in plant growth and developmental processes at varying concentrations. The most known molecular mechanism for auxin-mediated gene expression is based on the TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALLING F-BOX PROTEINS (TIR1/AFBs) pathway. The TIR1/AFB pathway primarily involves three components: the (SKP1-CUL1-F-box) SCFTIR1/AFB receptor complex, the Aux/IAA repressor proteins, and ARFs. The latter can be either transcriptional activators (class A ARFs) or transcriptional repressors (class B/C ARFs). In the absence of auxin, the activity of the transcription factor ARF is toned down by the transcriptional repressor Aux/IAA protein (Leyser, 2018). In the presence of auxin, TIR1/AFB proteins bind to the transcriptional

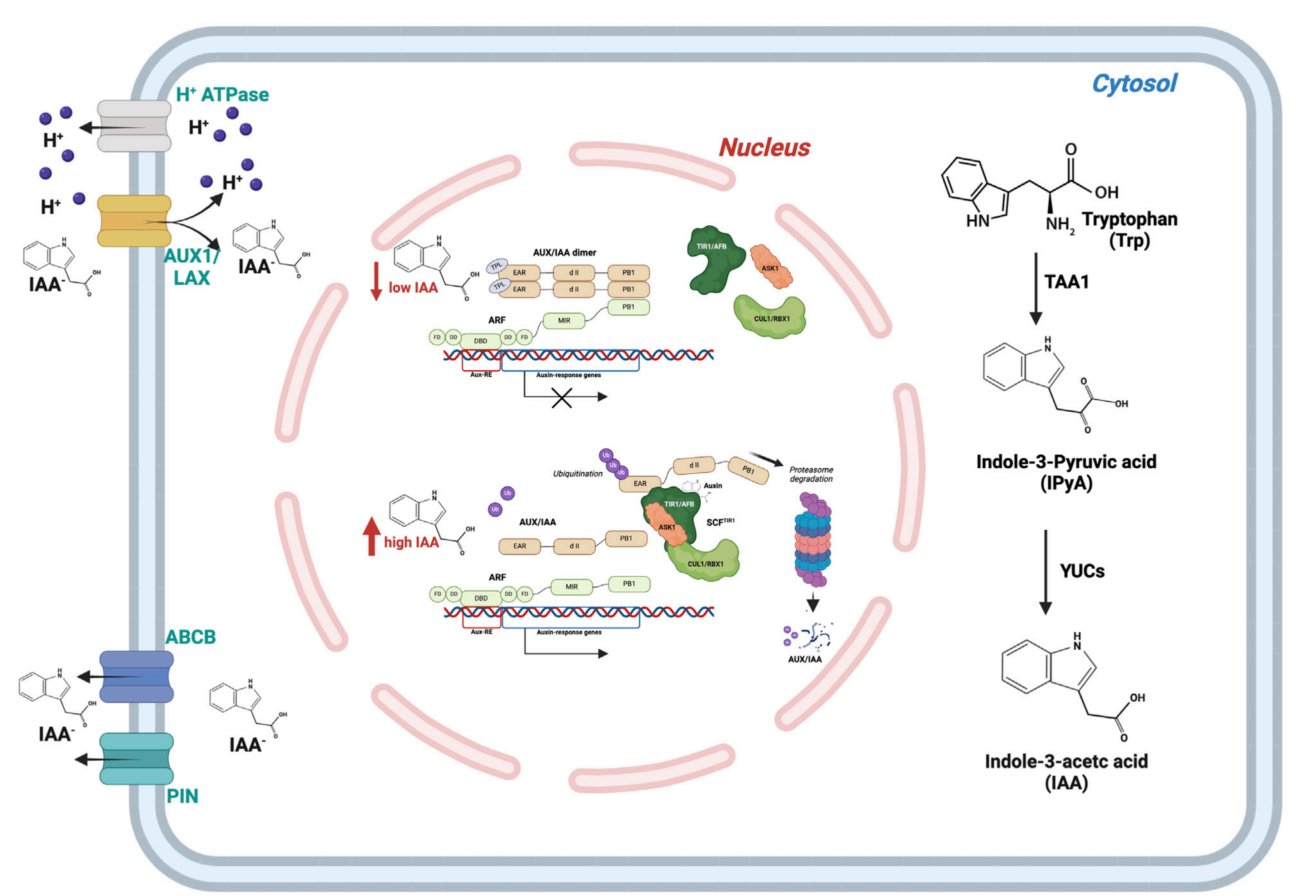

FIGURE 1
Auxin concentration in the cell is regulated by three different pathways: biosynthesis, transport, and signal transduction. Cytosolic biosynthesis is mainly performed by the TAA1/YUC pathway. Auxin concentration in the cell can be modulated through PIN and ABCB membrane proteins. The auxin signal is transduced through the mediation of ARF-AUX/IAA transcription factors.

repressors Aux/IAA inducing their degradation via the 26S proteasome, allowing transcriptional regulation by ARFs (Figure 1).

Auxin can also be perceived in cells by the apoplastic receptor ABP1 (AUXIN BINDING PROTEIN1) and its homologues ABL1 and 2 (ABP1 LIKE1 and 2). Those proteins bind auxin together with the Transmembrane Receptor Kinases (TMKs), inducing an ultrafast phospho-response (Friml et al., 2022; Yu et al., 2023). TMK proteins phosphorylate also plasma membrane H$^+$-ATPases, important regulators of growth (Pacifici et al., 2018; Lin et al., 2021), and ABA INSENSITIVE 1 and 2 (ABI1 and ABI2), negative regulators of Abscisic Acid response (Yang et al., 2021). Although this signalling pathway is newly discovered and has not yet been correlated with abiotic stress responses, these data permit speculation that the ABP1/TMK pathway might be primarily involved in the modulation of growth in response to abiotic stresses.

3 GCC is leading to harsh environmental conditions that induce stress responses in plants

Salinity and drought are among the main abiotic stressors that impact plant health worldwide. Both affect soil water potential, leading to insufficient water uptake by plant roots and causing ion imbalance (Cruz de Carvalho, 2008; Mickelbart et al., 2015; Ribba et al., 2020; Verma et al., 2022). Besides, drought leads to a progressive increase of HMs in soil, affecting plant growth (Tipping et al., 2003; Lequeux et al., 2010; Stirling et al., 2020). In this framework, the auxin response serves as a crucial hormone for the adaptation of plants to salinity, drought, and HM stress (Shi et al., 2014; Ribba et al., 2020), linking ROS signalling to physiological development. Indeed, these abiotic stresses trigger a significant increase in ROS, causing changes in many crucial cellular metabolic processes and reactions (Ahanger et al., 2017). Strategies to cope with these changes include maintaining ROS equilibrium, controlling stomata closure, generating proline, and adjusting root growth and structure (Dat et al., 2000; Geng et al., 2013; Verma et al., 2022; Scintu et al., 2023).

3.1 Modulation of auxin biosynthesis promotes tolerance to drought and salinity stress

Plants cultivated in salty environments exhibited elevated levels of YUC4, NIT1 and NIT2, which promote auxin production. Arabidopsis *NIT2* overexpressing lines have higher auxin levels only when grown under saline conditions, suggesting a specific role for this enzyme (Cackett et al., 2022). At the same time, auxin biosynthesis also modulates drought responses. Indeed, activation-tagged Arabidopsis mutants *yuc6-1D* and *yuc7-1D* are resistant to drought stress, while *YUCCA6* and *YUCCA7* loss-of-function mutants are more sensitive to water deficiency (Lee et al., 2012; Kim et al., 2013). Transgenic plants of potato (*Solanum tuberosum* cv. *Jowon*) and poplar (*Populus alba* × *P. glandulosa*) overexpressing the Arabidopsis gene *YUCCA6* showed enhanced drought tolerance, reduced water loss, and decreased levels of ROS (Kim et al., 2013; Ke et al., 2015). Furthermore, Arabidopsis *yuc1 yuc2 yuc6* triple mutants showed decreased auxin production, reduced drought stress resistance, and increased ROS levels (Shi et al., 2014), pointing out that an increase in auxin biosynthesis stimulates stress tolerance. However, a detailed characterization of transcription factors regulating *YUCCAs* expression in response to abiotic stress still lacks. Only recently, it was suggested that in rice (*Oryza sativa*), the MADS-box transcription factor OsMADS25, whose overexpression confers salinity tolerance, induces the expression of *OsYUC4,* promoting auxin biosynthesis to achieve stress resistance (Xu et al., 2018). This evidence further underlines the central role of auxin biosynthesis in salt and drought stress perception and tolerance (Figure 2).

3.2 Tolerance to drought and salinity stress requires repression of auxin signalling

Recently, it was demonstrated that in Arabidopsis, the auxin repressors IAA5, IAA6, and IAA19 positively regulate tolerance to drought stress, promoting stomata closure through the repression of the ABA-responsive transcription factor ABA OVERLY SENSITIVE3 (*ABO3*) expression. On the other hand, *iaa5 iaa6 iaa19* triple mutants exhibit reduced drought tolerance, fail to close stomata, and show increased *ABO3* transcript levels in drought conditions (Salehin et al., 2019). In rice, *OsIAA20* RNAi transgenic lines showed decreased proline and chlorophyll content, a significant reduction in stomata closure, and downregulation of the ABA-responsive gene *OsRab21*, which is involved in drought stress tolerance. Accordingly, transgenic plants overexpressing *OsIAA20* exhibited improved tolerance to abiotic stress and increased expression of *OsRab21* (Zhang et al., 2021). Overexpression of *OsIAA18* triggers enhanced salt and drought tolerance, increases ABA biosynthesis and signalling, and promotes proline biosynthesis (Wang F. et al., 2021). Drought and ABA treatments induce the transcription of *OsIAA6*, while *OsIAA6* overexpressing lines show improved drought tolerance (Jung et al., 2015). All these findings support the idea that *Aux/IAA* genes function as hubs integrating physiological development and molecular responses to environmental changes, highlighting that the upregulation of *Aux/IAA* mainly enhances plants tolerance to drought stress.

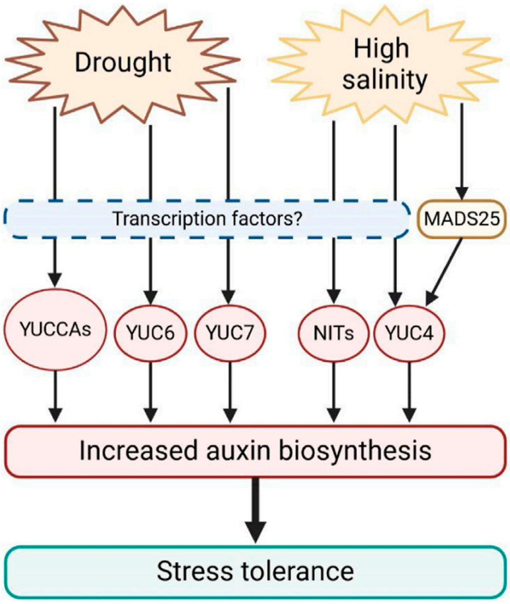

FIGURE 2
Schematic representation of the expression of auxin biosynthetic genes induced by drought and salt stress in plants. Drought and salt promote the transcription of YUCCAs and NITs genes, which in turn induce auxin biosynthesis. Increased auxin content stimulates stress tolerance. However, transcription factors translating stress signals to auxin biosynthesis still remain largely unknown.

In parallel, upon drought and salt perception, the expression of *ARFs* may vary in positive or negative ways (Bouzroud et al., 2018). Generally, it is thought that their downregulation improves plants resistance to stress. Silencing of *ARF2* in tomato (*Solanum lycopersicum*) triggers the upregulation of ROS scavenger and proline biosynthesis genes, conferring enhanced tolerance to abiotic stress (El Mamoun et al., 2023). Consistently, Arabidopsis *arf2* knockdown mutants accumulate ABA, resulting in increased stomata closing, reduced leaf transpiration, and improved stress tolerance (Meng et al., 2015). In addition, in tomato, *arf4* loss of function induces the expression of the ABA-related genes *SlABI5* and *SlSCL3* and shows significant alterations in stomata morphology and closing (Chen et al., 2021). Antisense and CRISPR/Cas9 downregulation of *SlARF4* promote root development, higher tolerance to salt and osmotic stress, reduced stomatal conductance, and increased leaf relative water content, corroborating the notion that *SlARF4* negatively regulates tolerance to salt and osmotic stresses (Bouzroud et al., 2020). Moreover, the loss of *AtARF7* and *AtARF19*, two well-known modulators of lateral root development, triggers a significantly reduced sensitivity to osmotic stress (Kalve et al., 2020).

Among transcription factors, C-repeat/dehydration-responsive element binding proteins (CBF/DREB) play an important and positive role in stress tolerance. In particular, *CBF/DREB* are upregulated in response to abiotic stress, and their overexpression is associated with drought tolerance (Lata and Prasad, 2011; Dong et al., 2017). Several CBF/DREBs directly promote the transcription of *Aux/IAAs*, such as *IAA5* and *IAA19*, in response to desiccation stress in Arabidopsis (Shani et al., 2017). These findings further support the notion of Aux/IAAs functioning as an intersection for the integration of stress responses (Figure 3).

Furthermore, the expression of transcription factors from the *NAC* family–*NAM* (no apical meristem) and *ATAF1/2* and *CUC2* (cup-shaped cotyledon)–is induced by abiotic stress, and they modulate gene transcription under drought conditions (Shao et al., 2015). It was shown that soybean (*Glycine max*) *GmNAC20* and *GmNAC11* overexpression in Arabidopsis plants enhances salt tolerance, promotes *DREB1A* expression, and modulates auxin signalling by acting on *ARF7* and *ARF19* expression (Hao et al., 2011). Similarly, it was demonstrated that

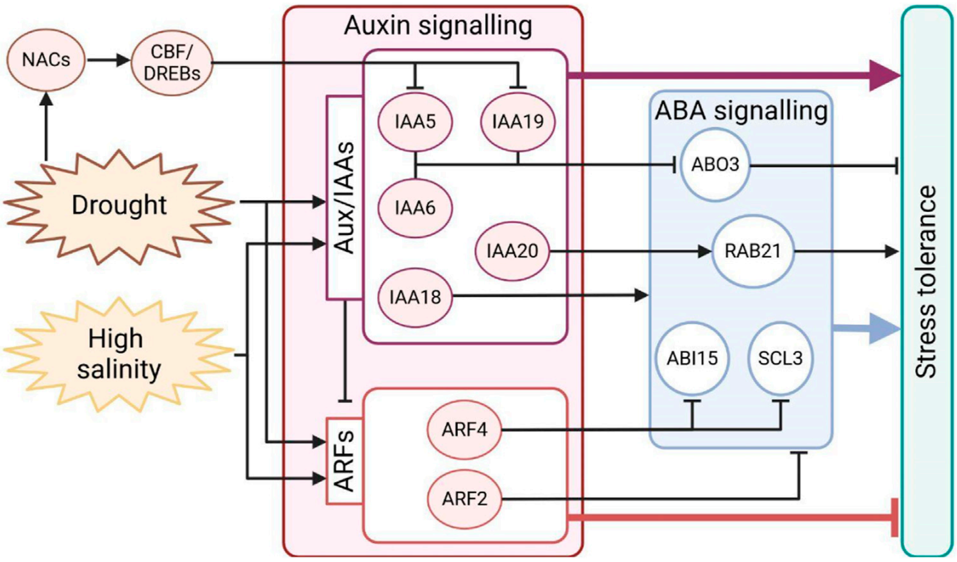

FIGURE 3
Schematic representation of auxin signalling regulation during drought and salt stress in plants. Both stresses promote the expression of the auxin-responsive genes *Aux/IAAs* and *ARFs*; however, the effective repression of ARFs could promote stress tolerance. NACs and DREBs are activated by stress, interact with each other, and modulate auxin signalling to achieve stress tolerance. ABA and auxin are connected by a tight interplay, partially illustrated in the figure. Expression of genes responsive to ABA can be induced or repressed by the auxin signalling component during stress responses. Arrows indicate positive regulation, and T-bars indicate negative regulation.

overexpression of pepper (*Capsicum annuum*) *NAC46* in Arabidopsis transgenic lines enhances resistance to drought and salt, increasing the expression of *IAA4* (Ma et al., 2021). It is worth mentioning that a tight connection exists between auxin, *NAC* transcription factors, and abiotic stress responses, as *NAC2* is induced by salt stress and its expression is abolished in *tir1-1* mutants in Arabidopsis (He et al., 2005).

3.3 Auxin transport as a key regulator for salt stress tolerance

Auxin activity and transport have been widely associated with root development. In this organ, auxin distribution is strictly related to cell developmental stages, as a maximum of auxin maintains stem cell activity, whereas a minimum prompts cells to differentiate (Sabatini et al., 1999; Blilou et al., 2005; Di Mambro et al., 2017). Being in direct contact with soil, roots are the first organ in plants to perceive drought and salinity stresses and to be subjected to stress-dependent growth inhibition. Auxin regulates root growth, promoting cell division in the root meristem, a region located at the root tip where a set of self-renewal stem cells support continuous growth (Di Mambro et al., 2018). It has been recently shown that salinity stress represses root development, promoting the exit of cells from the meristem and, hence, cell elongation and differentiation, activities dependent on variation in polar auxin transport (Scintu et al., 2023). For the reasons above, roots have been largely utilised as model systems to study the effect of drought and salt stresses on auxin transport. First evidence that auxin distribution varies in response to salinity stress has been given by the indirect auxin sensor DR5, which shows a maximum of activity in the root stem cell niche. DR5 activity is largely decreased by salt exposure, most likely due to a decreased expression of the polar auxin transporter PIN1, 2, and 3 (Liu et al., 2015; Fu et al., 2019; Smolko et al., 2021). Little is known about the molecular basis governing the salt-dependent inhibition of *PINs* expression. Recently, it has been shown that short exposures to salt stress promote the expression of the SHORT HYPOCOTYL2 *(SHY2)/IAA3* gene, a negative regulator of the polar auxin transport in the root meristem, via induction of cytokinin biosynthesis in the meristem (Dello Ioio et al., 2008; Dello Ioio et al., 2012; Scintu et al., 2023). This finding provides an enthralling possibility that, at first, salt represses plant growth by inhibiting auxin signalling and, hence, auxin distribution, altering cell developmental stages. In the future, it will be key to understand whether and how variation in auxin distribution in roots might infer shoot organ growth inhibition in response to salt stress.

Once perceived salt stress, root development adapts to this re-establishing growth. The Salt Overly Sensitive (SOS) pathway is pivotal in this process, as *sos* mutants show hypersensitivity to salt stress (Yang and Guo, 2018). Over salt exposure, plant cells increase cytosolic Ca^{2+} concentration, leading to the activation of the calcium-binding protein SALT OVERLY SENSITIVE 3 (SOS3) (Yang and Guo, 2018). SOS3 recruits on the plasma membrane the serine/threonine protein kinase SOS2 that activates the Na^+/H^+ antiporter SOS1 via phosphorylation, decreasing the intracellular Na^+ concentration (Yang and Guo, 2018). Interestingly, *sos* mutants oversensitivity to salt stress is partly dependent on PIN regulation by this stress (Zhao, 2018). It has been recently found that SOS2 phosphorylates and stabilises in response to the salts PLT1 and PLT2 (Hao et al., 2023), two auxin-dependent transcription factors regulating auxin distribution via the promotion of *PINs* expression (Blilou et al., 2005). These data open the possibility that plants adapt to salt stress by regulating PIN-dependent auxin distribution, hence promoting growth in adverse conditions (Figure 4). Whether this mechanism is favourable only for root development is still a matter of discussion.

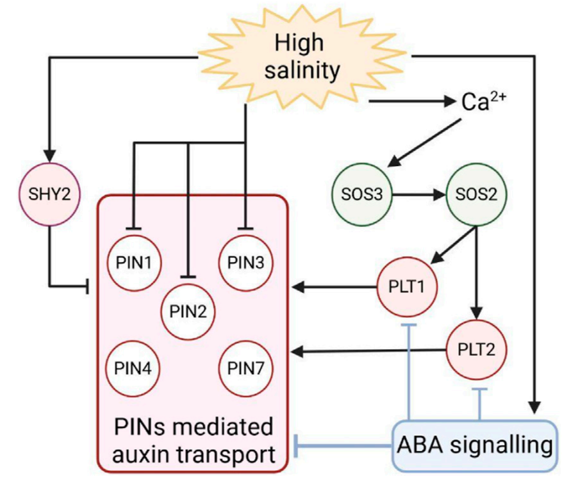

FIGURE 4
Schematic representation of PINs-mediated auxin transport regulation during salt stress. Responses to salt treatment involve different pathways that regulate the expression of PINs to modulate auxin distribution in roots. Arrows indicate positive regulation, and T-bars indicate negative regulation.

The maintenance of root growth under water stress conditions has been largely studied in rice and tomato. This is mediated by a synergistic action of ABA and auxin, in which the former hormone accumulates first in the root tip and modulates auxin transport through regulation of AUX/LAX and PIN, which enhances proton secretion to preserve the root growth from severe water stress. In this context, the involvement of transcription factors in auxin transport remains to be fully unveiled, but some evidence gives them a role in fine-tuning the response to drought and salinity stress. The WRKYs transcription factors are reported as important regulators of abiotic stress tolerance (Jiang and Deyholos, 2006; Zhou et al., 2008; Niu et al., 2012; Song et al., 2016). In tomato, overexpression of *SlWRKY3* provides tolerance to salinity and, consequently, reduced oxidative stress and proline contents compared to wild-type. Interestingly, those plants show upregulation of LAX3 (auxin influx carrier) proteins, providing a role for this auxin influx carrier in salt and drought stress tolerance (Hichri et al., 2017).

Salt and drought stress inhibit root complexity, repressing lateral root elongation via ABA (De Smet et al., 2003; Lu et al., 2019). It has been shown that the emergence and elongation of lateral roots are strictly dependent on the formation of an auxin maximum that is guided by PINs cellular localization (Cavallari et al., 2021). Long exposure to high salinity stress promotes ABA synthesis and signalling in roots (Geng et al., 2013). Interestingly, ABA is able to repress the expression of several PIN proteins, such as *PIN1, 3, 4*, and *7*, and the expression of *PLT1* and *PLT2* in both the elongation zone of the primary root and lateral roots (Promchuea et al., 2017). As lateral root formation also depends on auxin accumulation and distribution in the meristem, the ABA/auxin module might represent a checkpoint for defining root architecture in response to salt stress. Further studies will elucidate the intricate connection between these two hormones to regulate root architecture in response to salinity and drought stress.

3.4 miRNAs represent a central hub in auxin-dependent regulation of drought and salt stress responses

In recent years, ~21–24 nucleotide-long single-strand microRNAs (miRNAs) have emerged as fundamental players in plant development control (Bertolotti et al., 2021). Recent studies on Arabidopsis have shown that the activity of these small macromolecules is required for regulating the response to several environmental stresses, including salt, drought, and HMs stresses (Zhang et al., 2022). Interestingly, numerous of these stress-related miRNAs target the mRNA of auxin-related genes. The first evidence of auxin-related miRNAs regulating development comes from miR393, targeting *TIR1/AFB* auxin receptors (Chen et al., 2011). The expression of this miRNA is induced in response to several stresses, including salt and drought stress, in several crops, suggesting a fine-tuning mechanism to control growth in response to these stresses (Chen et al., 2015; Bai et al., 2017; Yuan et al., 2019). miR160 targeting *ARF10, 16*, and *17* has been found to be a central hub for mediating plastic development after exposure to several stresses in a multitude of species, such as wheat, rice, and barley (Reinhart et al., 2002; Liu et al., 2010; Hao et al., 2022).

In most of the species, drought stress promotes *MIR160* expression, dampening *ARFs* expression levels; on the contrary, salt stress represses its expression (Hao et al., 2022). When exposed to high salinity, *MIR160* transcription is inhibited in rice and in citrus plants (Huang et al., 2016; Dubey et al., 2020; Zhou et al., 2020). The regulation of *MIR160* in response to stresses highlights the importance of auxin activity in plant adaptation to the environment, as this is fundamental for both regulating lateral root development and counteracting ROS accumulation (Bertolotti et al., 2021). Interestingly, auxin-related miR167 is involved in *ARF6* and *ARF8* post-transcriptional regulation, and miR390 is involved in the generation of tasiRNA (TAS3-derived trans-acting short-interfering RNA), which targets *ARF2, ARF3*, and *ARF4* (Montgomery et al., 2008; Marin et al., 2010) and has been shown to be regulated by abiotic stresses (Wang et al., 2005; Gutierrez et al., 2009; Khan et al., 2011).

In Arabidopsis, *MIR167* expression is upregulated in response to most of the stresses, but in monocots such as maize, rice, and wheat, it is downregulated (Zhang N. et al., 2018), pointing out how the different ARFs acquired specific roles during evolution.

Several miRNAs whose expression responds to stresses are indirectly affecting auxin dynamics. An example of this is given by miR165 and 166, targeting the transcription factors *HOMEODOMAIN LEUCINE ZIPPER III (HD-ZIPIII)* (Bertolotti et al., 2021). HD-ZIPIIIs regulate both the expression of *ARF5* and the synthesis of cytokinin (Dello Ioio et al., 2012; Müller et al., 2016), which downregulates the expression of PIN genes in the root. *MIR165* and *166* expression is tightly linked to ABA regulation (Yan et al., 2016; Ramachandran et al., 2018; Yang et al., 2019), constituting a link between auxin, cytokinin, and this hormone. Interestingly, over-expression and downregulation of these miRNAs via MIMICRY technology confer tolerance to salt and/or drought stresses (Jia et al., 2015; Scintu et al., 2023).

The exact role of these microRNAs in response to stresses is still a matter of discussion; however, the reported examples highlight the intrinsic nature of these macromolecules in the regulation of mRNA target dosages (Scintu et al., 2023), a field of research that might represent a crucial point for the generation of plants tolerant to abiotic stresses.

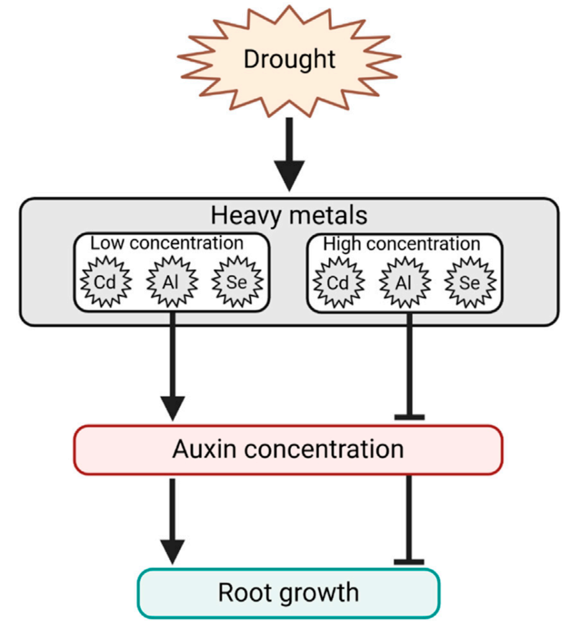

FIGURE 5
Hypothesized HMs dose-dependent response model regulating auxin concentration and, consequently, root growth. Arrows indicate positive regulation, and T-bars indicate negative regulation.

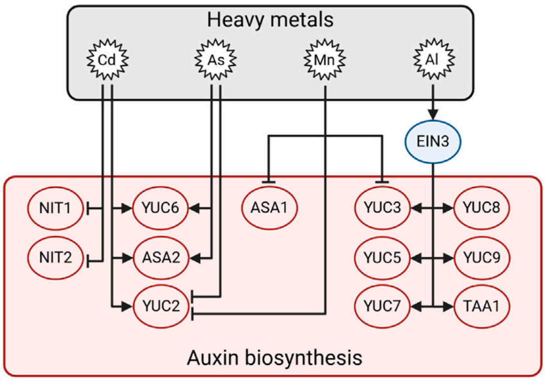

FIGURE 6
Illustration of the proposed model underlying the auxin biosynthetic pathway in the presence of Al, As, Cd, and Mn. Arrows indicate positive regulation, and T-bars indicate negative regulation.

3.5 Auxin contributes to heavy metals tolerance

Water scarcity is among the most critical effects induced by GCC. Its persistence can lead to an increase in ion concentrations, determining a rise in HMs in soil. Indeed, drought increases the amount of nonessential elements such as aluminium (Al), arsenic (As), cadmium (Cd), and selenium (Se), promoting their accumulation in soil and causing detrimental consequences for plants. Negative effects include low biomass production, chlorosis, reduced photosynthesis, altered water balance, and nutrient assimilation (Finnegan and Chen, 2012; Sun et al., 2014; Ali and Gill, 2022). On the other hand, metals such as zinc (Zn), manganese (Mn), and nickel (Ni) have been classified as essential micronutrients that play a positive role in plant growth when present at optimal concentrations. However, excessive uptake could affect metabolic processes, leading to adverse effects on plants (Hassan et al., 2019; Li et al., 2019; Kaur and Garg, 2021).

The primary morphological response related to HMs stress is associated with reduced primary root length, decreased lateral root proliferation, and reduced leaf area. These morphological responses are associated with a deregulation of auxin homeostasis and gene expression in Arabidopsis, in which auxin is a crucial regulator of primary root growth and lateral root initiation and elongation (Overvoorde et al., 2010). However, the effect of HMs on root growth varies depending on the element and its concentration. For example, it was found that in the presence of mild Cd, auxin accumulation occurs in the root tips of Arabidopsis and barley, while at high Cd, auxin levels decrease (Hu et al., 2013; Demecsová et al., 2020). Similarly, the presence of Al promotes auxin accumulation in rice root apex, determining the inhibition of its elongation (Wang et al., 2019). Low and high concentration of Se, respectively, increased or decreased the auxin content in both the root and shoot of tobacco seedlings (Luo et al., 2019). This is due to both the increased expression of genes involved in the IAA biosynthetic pathway, as well as the enhanced activity of IAA oxidase leading to auxin catabolism, alongside the involvement of AUX transporters, which contribute to root auxin depletion. Altogether, these findings suggest that the auxin distribution can highly vary in relation to plant species, chemical elements, and concentrations (Figure 5). Interestingly, a mild or high accumulation of the element usually leads to a rise or inhibition of auxin content and, consequently, plant growth. This response at low doses of toxic substances, also described as hormesis, results in a stimulatory effect on plant growth and can be used to further investigate the underlying molecular mechanisms during stress responses (Calabrese et al., 2016; Małkowski et al., 2020).

3.5.1 HMs differentially regulate auxin biosynthesis

Recently, it was shown that different YUCCAs are involved in responses to HMs, which can even antagonise each other's effects depending on the plant species (Yan et al., 2016). In Arabidopsis hypocotyls, Cd stimulates the expression of *AtYUC6* while As suppresses it, leading to the promotion and inhibition of auxin production, respectively (Fattorini et al., 2017). Conversely, *OsASA2* and *OsYUCCA2* transcripts are upregulated by Cd and As in rice roots, which grow less than control ones (Ronzan et al., 2018). In addition, Arabidopsis *yuc6-1D* mutants are more tolerant to Ni stress than control plants (Cha et al., 2022). In tobacco (*Nicotiana tabacum*), Cd stress altered the auxin gradient by affecting auxin biosynthesis genes *NtYUCCA6*, *8*, and *9* (Luo et al., 2019). The ethylene-responsive transcription factor ethylene-insensitive 3 (EIN3) induces the expression of *AtYUC3*, *5*, *7*, *8*, *9* and *AtTAA1* upon Al treatment, triggering the repression of root development in Arabidopsis (Liu et al., 2016; Yang et al., 2019). On the other hand, *AtYUC2*, *3* and *AtASA1* expression is downregulated by manganese (Mn), which represses root elongation (Zhao et al., 2017). In sorghum (*Sorghum bicolor*), quick responses to Cd include increased expression of auxin biosynthetic genes such as *SbNIT1* and *SbNIT2*, while their expression is significantly repressed after 5 days of Cd treatment (Zhan et al., 2017). Overall, these data indicate that auxin biosynthesis is differentially regulated by different HMs and that it could be induced or repressed depending on the element (Figure 6).

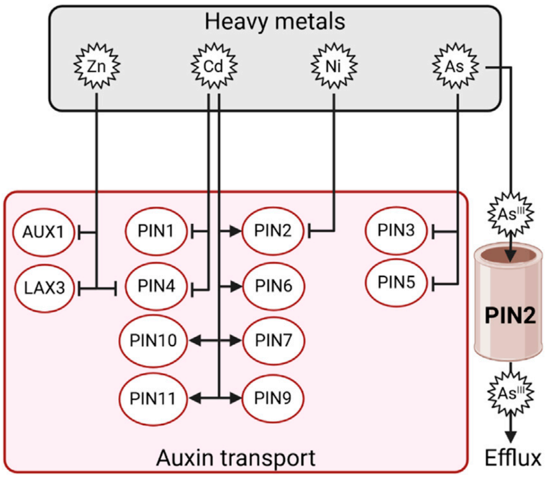

FIGURE 7
Schematic representation of the differential regulation of auxin transporters by Zn, Cd, Ni, or As. Arrows indicate positive regulation, and T-bars indicate negative regulation.

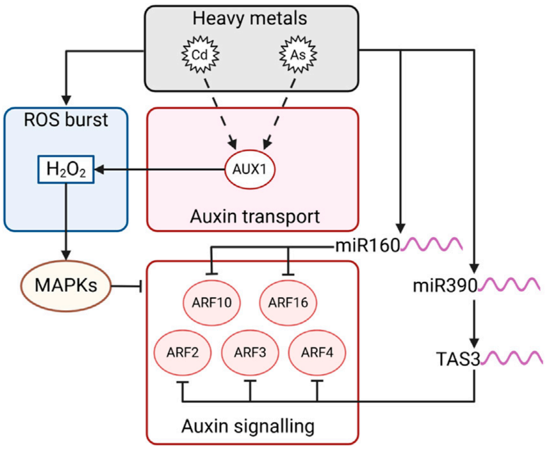

FIGURE 8
Schematic representation of the interplay among auxin signalling and ROS upon HMs stress. Arrows indicate positive regulation, and T-bars indicate negative regulation. Dashed lines represent multiple steps or unconfirmed direct interactions.

3.5.2 HMs affect auxin transport, impairing auxin homeostasis

Besides biosynthesis, HMs also impair auxin transport, affecting its spatial distribution and homeostasis. Indeed, Cd induces a downregulation of *PIN1* and *PIN4* expression in tobacco (Luo et al., 2019). Arsenic caused downregulation of *PIN3* and *PIN5* expression in both the roots and shoots of Brassica plants (Praveen et al., 2019). Similarly, Ni downregulated the expression of *PIN2* and inhibited the shoot-directed distribution of auxin in Arabidopsis (Lešková et al., 2020). *PIN2* overexpression in rice results in the restoration of basipetal IAA transport and inhibits ROS generation in Al-stressed plants (Wu et al., 2014). An interesting finding on PIN2 comes out from studies in Arabidopsis. In this species, *pin2* loss-of-function mutants show hypersensitivity to As(III). Surprisingly, *pin2* plants accumulate more arsenic species in root apices compared with wild-type seedlings, suggesting that PIN2 may function as a specific As(III) efflux transporter and not only as an auxin efflux facilitator (Ashraf et al., 2020). Root growth is altered in Arabidopsis exposed to Zn, which affects the expression of *AUX1, LAX3* (Sofo et al., 2017), and *PIN4* (Zhang P. et al., 2018), resulting in impaired auxin homeostasis (Wang J. et al., 2021). Altogether, these findings give an overview of the complex interaction existing between HMs and auxin in plants, which becomes even more intricate as other actors, such as ROS, play prominent roles in this crosstalk (Figure 7).

3.5.3 Auxin signalling during HMs stress is mediated by auxin-ROS crosstalk and miRNAs

The toxic effects of HMs ions are characterised by a tight auxin-ROS interplay in Arabidopsis, which is essential for stress response (Wang et al., 2015). Their phytotoxicity depends mainly on their high redox activity, which impairs the balance between the generation and degradation of ROS, leading to oxidative stress (Shahid et al., 2014).

Rice mutants for the auxin influx transporter *aux1* appear more sensitive to Cd stress due to the higher accumulation of ROS (Yu et al., 2015). In the roots of sorghum, Cd stress affects auxin and ROS homeostasis, triggering a decrease in root length proportional to the increase in Cd content in the medium. (Zhan et al., 2017). Among auxin transporters, Arabidopsis *aux1*, *pin1,* and *pin2* mutants were significantly sensitive to As (III) and developed shorter roots. On the other hand, *AUX1* was shown to be involved in the production of H_2O_2 (Krishnamurthy and Rathinasabapathi, 2013), which is known to be a molecular link between oxidative stress and auxin. H_2O_2 activates ANP1 (NPK1-like protein kinase), a specific class of stress-induced mitogen-activated protein kinases (MAPKs) upregulated by oxidative stress and able to repress auxin responsive promoter activity, causing displacement in auxin homeostasis (Kovtun et al., 2000). Interestingly, transcriptomic analysis on Kentucky bluegrass (*Poa pratensis*) treated with Cd revealed the contemporary deregulation of MAPKs signalling pathway and auxin-responsive genes such as *Aux/IAA* and *ARFs* upon stress perception (Xian et al., 2020). In parallel, the interactions between hub TFs and differentially expressed genes were investigated, and MADS25 was found to potentially interact with about 688 genes, comprising several auxin-related genes (Xian et al., 2020). This finding further highlights the key role of TFs in the regulation of HM stress tolerance. In pea seedlings, Cd-induced oxidative stress activated the peroxidase enzymes that lead to auxin oxidation and reduced its stability (Chaoui and El Ferjani, 2005). In barley root tips, it was shown that H_2O_2 acts downstream of IAA in root responses to Cd stress. As a consequence, a decrease in auxin concentration triggers a burst in ROS production, repressing the expression of genes involved in cell cycle regulation and root growth (Demecsová et al., 2020).

Another aspect of HMs-induced stress involves the regulation of miRNAs, key factors in modulating auxin homeostasis. Recent findings show that several miRNAs are upregulated by HMs and that they target components of the auxin signalling cascade, such as TIR1, AFBs, and ARFs (Gao et al., 2019; Du et al., 2022). This response involves the regulatory network that controls adventitious rooting,

TABLE 1 Most relevant TFs reported to be related to auxin regulation in response to abiotic stresses.

Gene name	Plant species	Function	Regulation by miRNA	Abiotic stress	Reference
ARF2	*Solanum lycopersicum*; *Arabidopsis thaliana*	Regulation of auxin signalling	miR390	Salt, drought, heavy metals	Bouzroud et al. (2018), El Mamoun et al. (2023), Montgomery et al. (2008), Marin et al. (2010)
ARF3	*Arabidopsis thaliana*	Regulation of auxin signalling	miR390	Salt, drought, heavy metals	Montgomery et al. (2008), Marin et al. (2010), Yoon et al. (2010)
ARF4	*Solanum lycopersicum*; *Arabidopsis thaliana*	Regulation of auxin signalling	miR390	Salt, drought, heavy metals	Bouzroud et al. (2018), Bouzroud et al. (2020) Chen et al. (2021), Montgomery et al. (2008), Marin et al. (2010), Yoon et al. (2010)
ARF6	*Solanum lycopersicum*; *Arabidopsis thaliana*	Regulation of auxin signalling	miR167	Salt, drought, heavy metals	Montgomery et al. (2008), Marin et al. (2010), Wang et al. (2005), Gutierrez et al. (2009)
ARF8	*Solanum lycopersicum*; *Arabidopsis thaliana*	Regulation of auxin signalling	miR167	Salt, drought, heavy metals	Montgomery et al. (2008), Marin et al. (2010), Wang et al. (2005), Gutierrez et al. (2009)
ARF10	*Arabidopsis thaliana*	Regulation of auxin signalling	miR160	Salt, drought	Montgomery et al. (2008), Liu et al. (2010), Wang et al. (2005)
ARF16	*Arabidopsis thaliana*	Regulation of auxin signalling	miR160	Salt, drought	Montgomery et al., 2008; Liu et al. (2010), Wang et al. (2005)
ARF17	*Arabidopsis thaliana*	Regulation of auxin signalling	miR160	Salt, drought, heavy metals	Montgomery et al. (2008), Gutierrez et al. (2009); Liu et al. (2010)
MADS25	*Oryza sativa*; *Poa pratensis*	Induction of auxin biosynthesis; interaction with auxin-related genes	-	Salt, heavy metals	Xu et al. (2018)
ABO3	*Arabidopsis thaliana*	Responsive to auxin signalling	-	Drought	Salehin et al. (2019)
RAB21	*Oryza sativa*	Responsive to auxin signalling	-	Drought	Zhang et al. (2021)
CBF/DREBs	*Arabidopsis thaliana*	Regulation of auxin signalling	-	Drought	Shani et al. (2017)
NAC20	*Glycine max*	Regulation of auxin signalling	-	Salt	Shao et al. (2015)
NAC11	*Glycine max*	Regulation of auxin signalling	-	Salt	Shao et al. (2015)
NAC46	*Arabidopsis thaliana*	Regulation of auxin signalling	-	Salt, drought	Ma et al. (2021)
WRKY3	*Solanum lycopersicum*	Regulation of auxin transport	-	Salt	Hichri et al. (2017)
EIN3	*Arabidopsis thaliana*	Regulation of auxin biosynthesis	-	Heavy metals	Yang et al. (2019), Liu et al. (2016)

based on the interaction of miR160, 167, and *ARF6, 8*, and *17*. Cd, Al, and As stress often induces deregulation of mRNAs, modulating root elongation, or lateral root formation by acting on auxin responsive gene regulation, signalling and degradation (Ding et al., 2011; Lima et al., 2011; Srivastava et al., 2013; Gao et al., 2019; Kuang et al., 2021; Pegler et al., 2021; Liu et al., 2022). In detail, *AtARF10* and *AtARF16* are targeted by miR160, which controls the development of the root cap (Wang et al., 2005; Khan et al., 2011), while miR390 has been reported to control the generation of tasiRNA (TAS3-derived trans-acting short-interfering RNA), which regulates lateral root growth by targeting transcription factors such as *AtARF2, AtARF3* and *AtARF4* (Marin et al., 2010; Yoon et al., 2010). miR528 targets IAA-alanine resistance protein 1 (*IAR1*), which is involved in the regulation of free cellular auxin, leading to an SCF-mediated protein increase (Li et al., 2019). In addition, the TIR1-F-box subunit is targeted by miR393 upon HMs stress.

Altogether these data underline that the fine tuning existing between auxin and ROS during HMs responses is obtained via different pathways (Figure 8).

4 Concluding remarks and future perspectives

Despite the recent progress in the molecular mechanisms employed by plants to face abiotic stresses, further studies are needed to fully clarify the role of auxin in these processes. It is still not clear, for example, whether variation in auxin dynamics might be coordinators of stress response or whether those are mere consequences of the activation of other pathways such as the ABA one. However, up to date, it is clear that the alteration of auxin dynamics in response to stresses results in the overall alteration of plant growth. Future studies will permit to define the exact role of auxin in response to stress.

Many transcription factors in Arabidopsis have been linked to auxin or abiotic challenges, but only a few have been demonstrated to directly regulate auxin dynamics in response to abiotic stimuli, such as drought and salt stress (Table 1). We searched the NCBI gene database of Arabidopsis using the keywords ‘transcription factor’, ‘auxin’, and ‘abiotic stress’. By analysing the overlapping

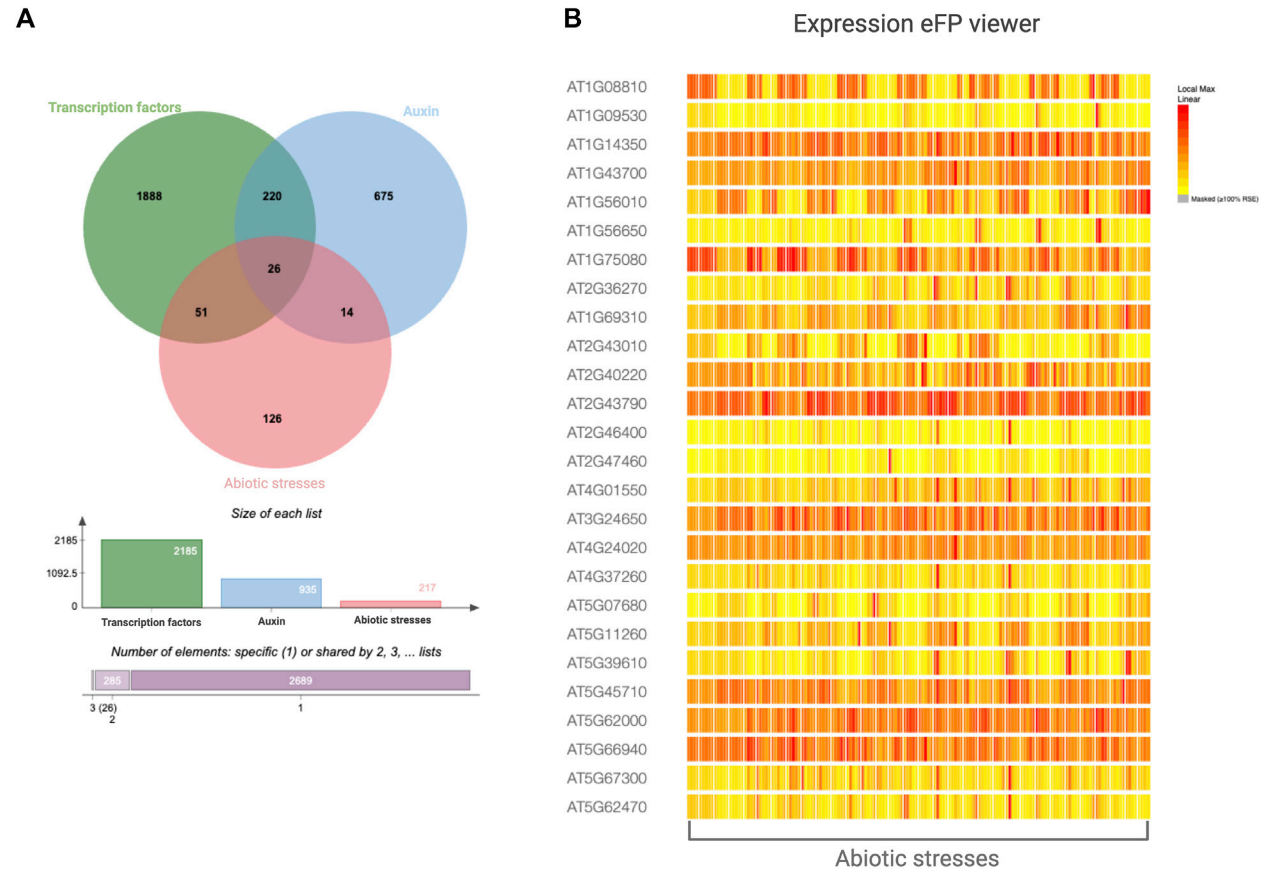

FIGURE 9
Transcription factors, auxin-related, and abiotic stress-related genes reported in the NCBI Gene database of *Arabidopsis*. **(A)** Venn diagram reporting the intersection among genes annotated as transcription factors, auxin-related, and abiotic stress-related. **(B)** The eFP viewer expression pattern of the core genes (26) depicted in the Venn diagram and reported in Supplementary Table S1.

data sets, we identified 26 transcription factors that were associated with all the searched terms (Figure 9A). Their transcriptional level largely varies across the different abiotic stresses (Figure 9B; Supplementary Table S1). We believe that these promising transcription factors are of primary interest for future research aimed at investigating their involvement in modulating auxin responses to abiotic stressors in both model and crop plant species.

Understanding the complex network of transcription factors regulating auxin biosynthesis and signalling could help find new biotechnological approaches to deal with adverse environmental conditions, hopefully leading to the identification of useful traits that might improve plant adaptation and resilience to GCC. Besides, modulation of miRNAs to alter ARF abundance during abiotic stress and the integration of new technologies such as CRISPR to edit auxin-related genes in crop species are also potential agricultural applications for improving stress tolerance. The use of different research tools such as expression profiling, mutant screening, microarrays, proteomics, system biology, and bioinformatics can offer a powerful platform for the identification as well as characterization of various molecular pathways involved in auxin-mediated HMs stress tolerance and cross-talk with other phytohormones and signalling molecules as ROS in plants.

Author contributions

DM: Conceptualization, Writing–original draft, Writing–review and editing. PB: Conceptualization, Writing–original draft, Writing–review and editing. SS: Conceptualization, Writing–original draft, Writing–review and editing. GY: Conceptualization, Writing–original draft, Writing–review and editing. GP: Conceptualization, Writing–original draft, Writing–review and editing. RD: Conceptualization, Writing–original draft, Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fgene.2024.1394091/full#supplementary-material

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