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AUXINS AS REGULATORS OF GROWTH AND DEVELOPMENT OF CEREAL CROPS UNDER ABIOTIC STRESSES: A REVIEW

Lesya Voytenko*, **Iryna Kosakivska**

Department of Phytohormonology, M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

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Abstract. Global climate change and population growth are driving a significant increase in the demand for food products. In response, there is a growing focus on cereal plants, particularly in identifying ways to enhance their resilience and productivity. Phytohormones are key endogenous regulators of plant physiological and metabolic processes under both normal and stressful conditions. They are effectively employed in new biotechnological approaches aimed at improving and directing plant productivity. Auxins, in particular, are natural hormones that play a crucial role in regulating plant growth and development across various environmental conditions. Auxin homeostasis and function are closely tied to its biosynthesis, degradation, transport and the formation of hormone conjugates. The aim of this revew is to analyze and summarize recent scientific findings on the role of auxins in regulating growth, development and adaptation of cereals to abiotic stresses. This review provides essential information on auxin biosynthesis, signaling, transport and functional activity. It also summarizes findings on auxin interactions with other phytohormones, such as cytokinin, abscisic acid, salicylic acid and gibberellins. The role of auxins in adapting cereals to drought, salinity, temperature extremes and heavy metal pollution is highlighted. Special attention is given to new biotechnological strategies for enhancing stress tolerance and yield, such as the use of exogenous auxins for pre-sowing seed priming and foliar treatments in cereals.

Keywords: *Indole-3-acetic acid, phytohormones, cereals, abiotic stress, growth, adaptation.*

****Corresponding Author:*** *Lesya Voytenko, Department of Phytohormonology, M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine, e-mail:* lesyavoytenko@gmail.com

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1. Introduction

Global climate changes and the increasing global population are driving a significant demand for food products. This has led to a particular focus on researching cereals and regulating their resistance and yield. Phytohormones are vital endogenous regulators of physiological and metabolic processes that influence plant growth under both normal and stressful conditions. They are widely used in biotechnological approaches to enhance plant productivity in targeted ways (Kosakivska *et al*., 2022a, 2024a, 2024b). Auxins, as natural phytohormones, play a crucial role in regulating plant growth and development under various growth conditions (Enders & Strader, 2015; Woodward & Bartel, 2005). Chemically, auxins are weak organic acids with an aromatic skeleton and a carboxylic acid group (Figure 1). Most natural auxins, such as indole-3-acetic acid (IAA), 4-chloroindole-3-acetic acid (4-CI-IAA), indole-3-butyric acid (IBA)

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and indole-3-propionic acid (IPA), contain an indole ring. However, phenylacetic acid (PAA) and phenylbutyric acid (PBA) lack this structure (Bajguz & Piotrowska, 2009; Korasick *et al*., 2013).

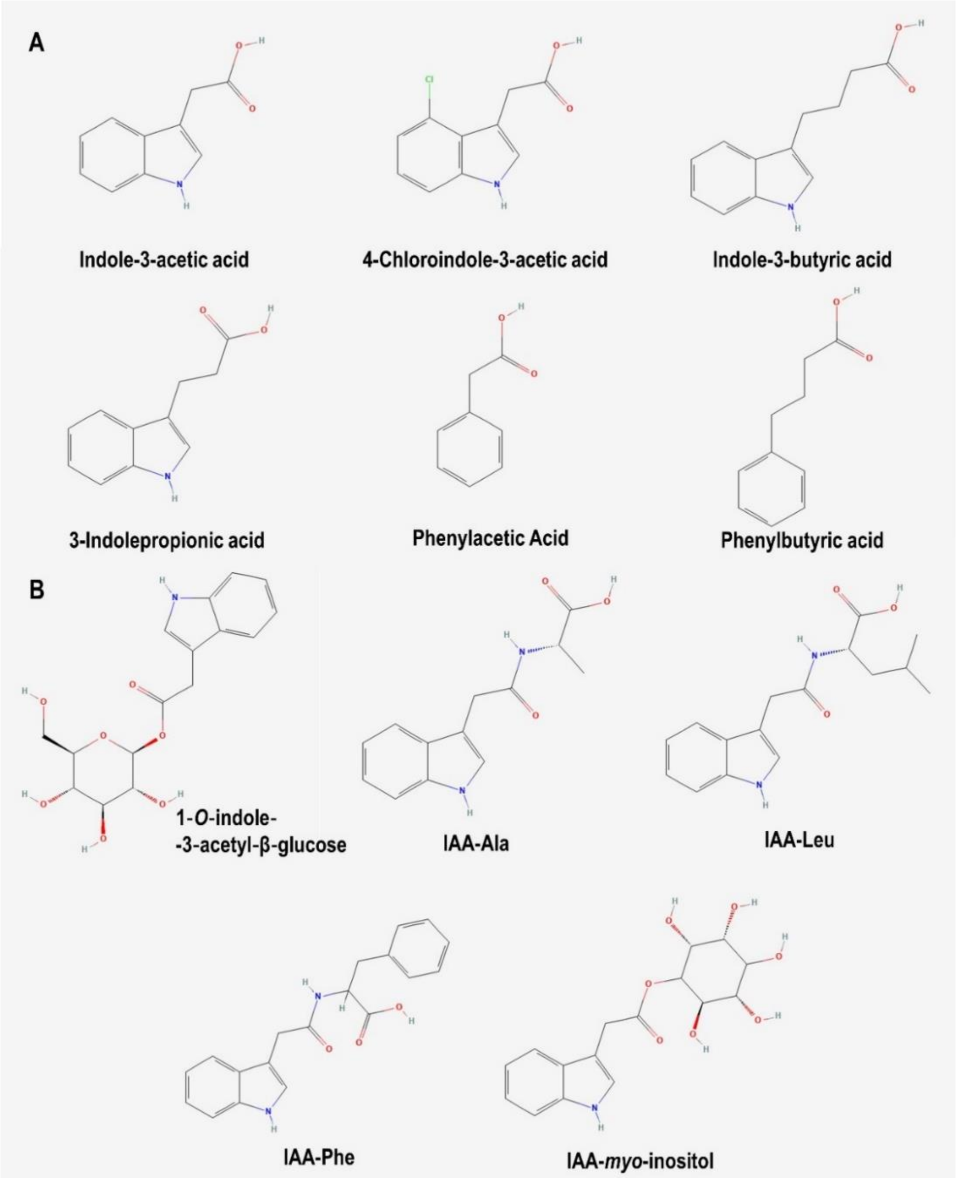

Figure 1. Natural auxins (A) and the most common conjugates of IAA (B)

IAA is the most abundant and active auxin, found in bacteria, algae, fungi, spore plant, seed plants, insects and even humans (Cooke *et al*., 2002; Kosakivska *et al*., 2016; Ross & Reid, 2010). Other active auxins include 4-Cl-IAA, IBA and PAA (Figure 1A) (Gomes & Scortecci, 2021; Simon & Petrášek, 2011; Sun *et al*., 2023; Tivendale *et al*., 2012). Initially believed to be exclusive to species of the *Fabeae* genus (Lam *et al*., 2016; Ribalta *et al*., 2019), 4-Cl-IAA is now recognized as a key signaling molecule in regulating inflorescence senescence in *Avena sativa* L. (Dziurka *et al*., 2019). IBA, an auxin precursor, is converted to IAA during β oxidation in peroxisomes (Strader *et al*., 2011). Structurally, IBA resembles IAA but has two additional methylene groups in its side chain (Damodaran & Strader, 2019; Dong et al., 2018). Although less abundant than IAA, IBA is more effective in specific function, such as promoting adventitious root development (Aihebaier *et al*., 2019; Fattorini *et al*., 2017). However, its role in auxin signal transduction remains unclear.

PAA, another natural auxin, is present in various plant taxa (Perez *et al*., 2023). Its biological activity in cereals such as oats, barley, wheat and maize - and in many dicotyledonous and vascular plants - is lower than that of IAA, despite its higher concentration (Sugawara *et al*., 2015; Wightman & Rauthan, 1974; Wightman & Lighty, 1982). PAA's physiological effects include root system formation (Perez *et al*., 2023) and elongation of cereals coleoptiles (Sugawara *et al*., 2015). Exogenous PAA application improves resistance to pathogens, whereas elevated IAA levels may increase pathogens susceptibility (Irmisch *et al*., 2015; Kunkel & Harper, 2018).

In plant tissues, active forms of auxins constitute approximately 25% of the total auxin content. Among auxin conjugates, esters of simple and long-chain carbohydrates, as well as amide-linked conjugates with amino acid, peptides and proteins have been identified (Korasick *et al*., 2013; Ludwig-Müller, 2011). Conjugation of IAA with aspartate (Asp), cysteine (Cys), histidine (His), isoleucine (Ile), lysine (Lys), proline (Pro), tryptophan (Trp) and valine (Val), various alcohols and sugars serves as a mechanism for hormone inactivation. In contrast, conjugates of IAA with alanine (Ala), leucine (Leu), phenylalanine (Phe), asparagine (Asn), glutamine (Gln), glutamic acid (Glu), glycine (Gly), methionine. (Met), serine (Ser), threonine (Thr) and tyrosine (Tyr), myo-inositol and peptides act as temporary storage forms. These conjugates can release free IAA through hydrolysis (Casanova-Sáez & Voß, 2019; Olatunji *et al*., 2017). Additionally, IAA conjugates with glucose, aspartic acid, oligosaccharides, nucleic acids, peptides, glycans and proteins function as transport forms of auxin (Korasick *et al*., 2013). The most common conjugates of IAA (Figure 1B) include 1-*O*-indole-3-acetyl-*β*-D-glucose, alanyl-IAA, leucyl-IAA, phenylalanyl-IAA, IAA-*myo*-inositol (Bartel, 1997; Kowalczyk *et al*., 2003; Ludwig-Müller, 2011). For IBA, prevalent conjugates include IBA-glucose as well as amide- and ester-linked forms (Damodaran & Strader, 2019; Sherp *et al*., 2018; Tognetti *et al*., 2010). In maize and rice grains, ester-linked IAA-sugar conjugates have been identified as source of IAA during germination. Hydrolases that cleave the ester bond between IAA and glucose facilitate this process (Ishimaru *et al*., 2013; Jakubowska & Kowalczyk, 2004, 2005; Kai *et al*., 2007). In our review, we focus on the role of auxins in cultivated cereals, summarizing recent scientific findings on their involvement in regulating growth, development and adaptation to abiotic stresses in these crops.

2. Biosynthesis, Signalling and Transport

Auxin biosynthesis occurs through both tryptophan (Trp)-independent and Trp-dependent pathways (Casanova-Sáez & Voß, 2019; Korasick *et al*., 2013; Mano & Nemoto, 2012; Zhao, 2012, 2018). The Trp-independent pathway is thought to be evolutionarily older and functions continuously during plant growth. It provides a baseline level of auxin and is largely unaffected by internal or external factors. The key enzymes of this pathway include cytosolic indole synthase (Nonhebel, 2015; Wang *et al*., 2015) and α tryptophan synthase (Bartel, 1997). The Trp-dependent pathway, by contrast, is activated at critical stages of plant development - such as embryogenesis, seed germination, flower formation and recovery from damage - when additional auxin is required (Cheng & Zhao, 2007; Mateo-Bonmatí *et al*., 2019). Most plants utilize a two-step Trp-dependent TAA/YUC (TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS/YUCCA) pathway for auxin biosynthesis (Figure 2). Other IAA biosynthesis pathways, while conserved, are considered functionally less significant in cereals compared to the TAA/YUC pathway (Korasick *et al*., 2013; Mano & Nemoto, 2012).

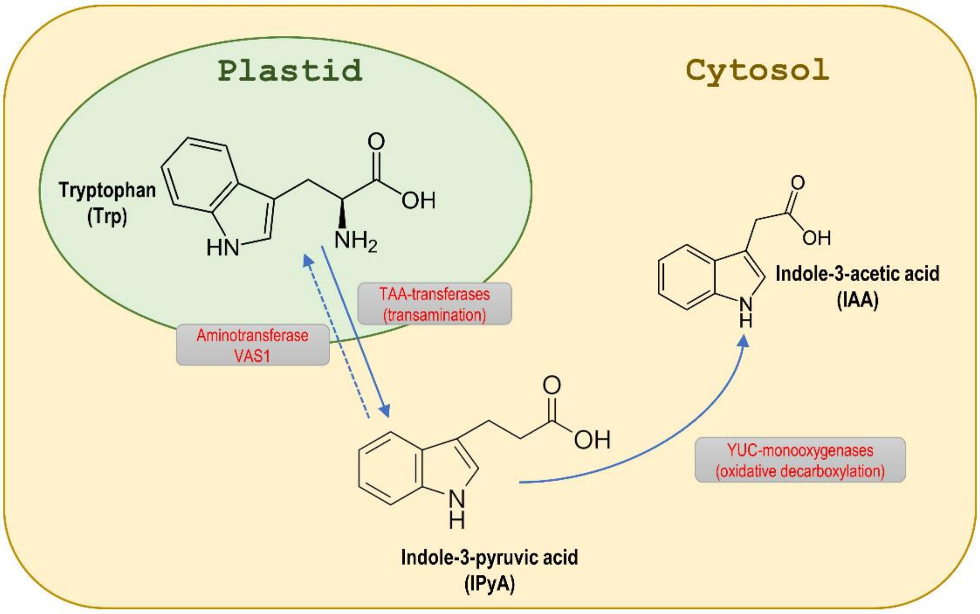

Figure 2. The two-step tryptophan (Trp)-dependent TAA/YUC pathway of auxin biosynthesis in plants. The first step involves the cleavage of the amino group by aminotransferases of the TAA family in plastids, resulting in the formation of indole-3-pyruvic acid (IPyA). This reaction, catalyzed by TAA, is reversible, with its direction determined by substrate availability. When IPyA levels are high, another aminotransferase, REVERSAL OF SAV3 PHENOTYPE1 (VAS1), converts IPyA back to Trp. The second step, oxidative decarboxylation of IPyA, is catalyzed by flavin-containing monooxygenases of the YUC family, typically occurring in the cytoplasm. NADPH and molecular oxygen act as co-substrates in this reaction, producing indole-3-acetic acid, carbon dioxide and water

Enzymes, receptors and transporter proteins involved in auxin biosynthesis are localized in chloroplasts, cytoplasm, endoplasmic reticulum membranes and mitochondria. Meanwhile, IAA itself and its metabolites are transported and stored in the apoplast and vacuoles (Ljung, 2013; Mateo-Bonmatí *et al*., 2019). Auxin synthesis primarily occurs in the apical meristem of shoots and roots, as well as in young shoots and leaves (Amanda *et al*., 2022; Olatunji *et al*., 2017; Wang *et al*., 2015).

The majority of IAA conjugates are formed through the direct attachment of the auxin molecule to various compounds (Ljung, 2013). Conjugate synthesis predominantly occurs in the cytoplasm before their distribution within cells and between plant organs. Auxin is temporarily or permanently inactivated through conjugation with sugars, amino acids or peptides via glycosyl ester and amide bonds (Normanly, 2010). The primary product of auxin inactivation is 2-oxoindole-3-acetic acid (OxIAA), which has been identified in algae, mosses, gymnosperms and angiosperms (Zhang & Peer, 2017). The concentration of IAA catabolites is proportional to the active auxin levels in tissues

(Novák *et al*., 2012) and increases in response to the application of exogenous IAA (Kubeš *et al*., 2012). Several enzymes involved in auxin inactivation have been identified, including: CARBOXYL METHYLTRANSFERASE1 (IAMT1), which converts IAA into its inactive methyl ester (Takubo *et al*., 2020) and DIOXYGENASE FOR AUXIN OXIDATION 1 (DAO1), which converts IAA into 2-oxoindole-3-acetic acid (OxIAA) (Zhao *et al*., 2013b). In maize and rice, glycoside formation is catalyzed by UDP-glycosyltransferases (Jackson *et al*., 2001; Szerszen *et al*., 1994). Meanwhile, the synthesis of amide conjugates in rice and wheat is mediated by specific amino acid conjugate synthases from the GH3 (GRETCHEN HAGEN 3) family of enzymes (Jain *et al*., 2006; Jiang *et al*., 2020).

Local auxin maxima and minima, crucial for the formation of morphogenetic programs, are regulated by the direction and speed of transport flows (Korasick *et al*., 2013). The rate of IAA transport varies across plant organs. Thus, in cereal seedling coleoptiles, transport speed ranges from 8 to15 mm/h, whereas in roots, the rate is approximately 1 to 2 mm/h. In organs closer to the apical meristem of the stem, which is the primary source of auxins, both the concentration and transport speed of auxin are consistently higher (Lomax *et al*., 1995). In cereals, several auxin transport proteins have been identified (Figure 3), with their differential expression and localization modulating auxin transport (Wakema & Bennett, 2023). Among these, the transporter proteins AUX1 and LIKE AUX1 (LAX) play a role in regulating polar auxin transport, enhancing or attenuating local auxin accumulation. However, the specific role of AUX1, as well as ABCB transporters in cereals, remain poorly understood (Balzan *et al*., 2014; Zhu *et al*., 2022). Cereals also possess a unique set of PIN family transporter proteins, which may regulate shoot structure (Bennett *et al*., 2014; Huang *et al*., 2017; Zhu *et al*., 2022). In wheat, increased expression of the *TaPIN1-6* genes has been observed in the stem tip and young leaves, with the TaPIN1-6a protein localized to the plasma membrane. Reduced *TaPIN1s* gene expression in transgenic lines resulted in plants with a greater number of tassels, spikelets and higher yield compared to wild type (Yao *et al*., 2021). PIN9 proteins also influence shoot structure. In rice, *OsPIN9* gene expression has been detected in the root, stem base (Wang *et al*., 2009a), shoot vessels and tassel buds (Hou *et al*., 2021). Similarly, in maize, *ZmPIN9* gene expression has been recorded in roots and nodes, but not in tassel or ears (Forestan *et al*., 2012). In *Brachypodium distachyon*, the expression of *PIN1a*, *PIN1b* and *PIN11/SISTER OF PIN1* (*SoPIN1*) genes has been observed in various parts of the spike meristem, as well as in internal tissues, developing vascular strands and the epidermis (O'Connor *et al*., 2014). The functional role of PIN10 proteins in the architecture of grass shoot is not yet well understood. However, their specific regulation in inflorescence development has been reported in maize and rice. *ZmPIN10a* shows higher expression in male inflorescence, while *ZmPIN10b* exhibits enhanced expression in a 3 mm section of the female inflorescence (Forestan & Varotto, 2012). In rice, *OsPIN10a* is predominantly expressed in the stem and young panicles, whereas *OsPIN10b* expression is elevated in veins, sheaths and young anthers (Wang *et al*., 2009a). The expression of *ZmPIN8* in young maize kernels is higher than that of *OsPIN8* in rice kernels. In both cereals, the highest expression of this gene occurs in immature inflorescences, with activity decreasing in mature inflorescences. In contrast, in Arabidopsis, *PIN8* shows high expression in stamens but low activity in seeds and inflorescence (Matthes *et al*., 2019).

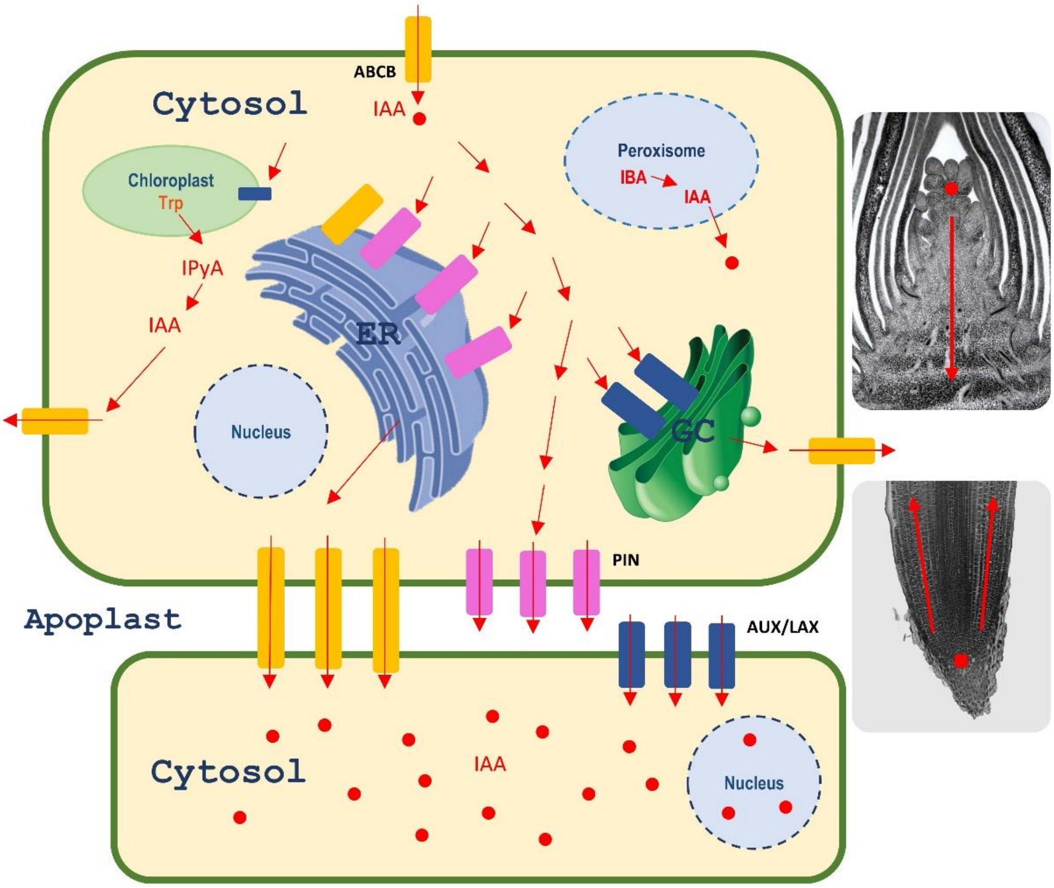

Figure 3. The primary pathways of polar auxin (IAA) transport in the shoot and root tips of cereals. Arrows indicate the direction of auxin transport mediated by specific transporters. PIN proteins are localized on the plasma membrane, while AUX/LAX and ABCB transporters are present both in the plasma membrane and within cellular organelles. Abbreviations: PIN-FORMED (PIN), ATP-BINDING CASSETTE subfamily B (ABCB) and AUXIN1/LIKE-AUX1 (AUX/LAX)

3. Functional activity

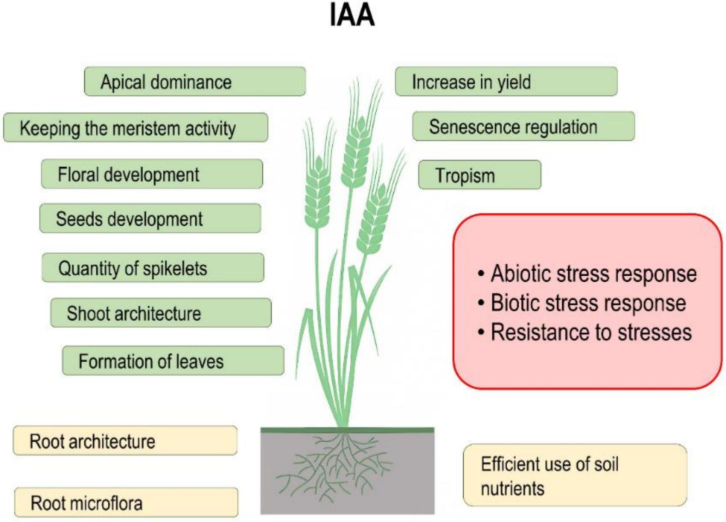

Figure 4. Auxin in regulation of cereal adaptation to environment

Auxins play a crucial role in plant development, influencing processes from early embryogenesis to fruit ripening and regulating organogenesis, which determines plant architecture (Cao *et al*., 2020; Paque & Weijers, 2016; Wakeman & Bennett, 2023; Zhang *et al*., 2022). The effect of auxin on plants depends on its concentration and distribution within organs and tissues, while phenotypic outcomes are influenced by tissue sensitivity and cellular perception of auxin signals (Vanneste & Friml, 2009). In monocotyledonous plants, auxins regulate the development of roots, shoots, leaves and vascular tissues, as well as the formation and maturation of panicles and spikelets (Figure 4) (Balzan *et al*., 2014; Wang *et al*., 2018).

PIN-FORMED (PIN) proteins are central to the spatiotemporal and asymmetric auxin distribution. For instance, overexpression of the *ZmPIN1a* gene in maize increases lateral root density and length, leading to enhanced root system development, reduced internode length, shorter spikes and inhibited above-ground growth. These changes improved yield under high planting density and increased resistance to drought, lodging and phosphate deficiency (Li *et al*., 2018). Auxins control shoot and root cell elongation by activating H+-ATPases localized on the plasma membrane (Du *et al*., 2020). Mutations in the *OsAUX1* gene resulted in decrease lateral root initiation in rice, while its overexpression increased lateral root formation (Zhao *et al*., 2015). Similarly, mutations in *OsIAA11*, *OsIAA13* and *OsIAA23* genes disrupted crown and lateral root development (Kitomi *et al*., 2012; Zhu *et al*., 2012), whereas overexpression of the *YUCCA* gene promoted lateral root growth (Yamamoto *et al*., 2007). The auxin transporter ZmPILS6, localized in the endoplasmic reticulum, regulates IAA distribution in primary maize roots (Cowling *et al*., 2024). Auxin promotes organ formation in cereal shoot meristems and regulates meristem activity, including the number and positioning of mature organs (Kellogg, 2022). However, auxin-induced shoot growth suppressed bud development by diverting sugars necessary for branching and stem growth (Kebrom, 2017). In maize and sorghum PGP mutants, auxin transport and cell elongation were impaired, leading to shortened internodes (Multani *et al*., 2003). Disruption of the *LAZY1* gene reduced gravitropism in rice shoots, resulting in branched plants (Yoshihara & Iino, 2007). In wheat, overexpression of *TaTAR2.1-3A*, a gene involved in Trp-dependent auxin biosynthesis, enhanced lateral root branching, increased plant height and spikelet number and improved yield (Shao *et al*., 2017). In rice, overexpression of *OsDRM1* delayed axillary bud growth, suppressed cell division and reduced plant height and root elongation. The application of exogenous auxin mitigated these effects (Chen *et al*., 2023).

Auxin also regulates floral organ development in rice and maize (Sazuka *et al*., 2009; Yoshida *et al*., 2012; Zhao *et al*., 2013b). In maize, auxin transporters ZmPIN1a and ZmPIN1b in the epidermal cell layer of inflorescences influence morphogenesis (Carraro *et al*., 2006). The *ZmLA* gene, which is auxin-responsive and light-repressed, is critical for shoot gravitropism and inflorescence development (Dong *et al*., 2013). Mutations in *SPI1* (*SPARSE INFLORESCENCE1*) in maize result in small spikelets with fewer grains (Gallavotti *et al*., 2008). In rice, overexpression of *OsPID* caused delayed adventitious root development, abnormal shoot growth and floral abnormalities, while its loss of function disrupted pistil and anther development (Morita & Kyozuka, 2007), while loss of *OsPID* function resulted in aberrant pistil and anther development (He *et al*., 2019; Xu *et al*., 2019). *OsPID* is proposed to regulate floral organ development, especially the stigma, by modulating polar auxin transport and interacting with OsMADS16 and/or LAX1 (Wu *et al*., 2020).

Auxin plays a critical role in seed development and yield in cereals (Basunia *et al*., 2021; Cao *et al*., 2020; Locascio *et al*., 2014). After pollination, endogenous IAA accumulates in rice spikelets (Uchiumi & Okamoto, 2010), regulating embryo size via *OsGE/CYP78B5* (Chen *et al*., 2015). In maize, auxin influences endosperm proliferation and cell differentiation during seed development (Bernardi *et al*., 2012; Forestan *et al*., 2010). Auxin also governs gynoecium growth, gamete formation and endosperm development in monocotyledonous cereals like maize, rice, sorghum and barley (Shirley *et al*., 2019), as well as dicotyledonous (Figueiredo *et al*., 2015, 2016; Salinas-Grenet *et al*., 2018).

4. Interaction with other phytohormones

The physiological effects of auxin are intricately linked to its interaction with other phytohormones (Mazzoni-Putman *et al*., 2021). Endogenous hormones play a central role in controlling the tillering process in cereals, while exogenous hormone applications influence bush bud growth by modulating the accumulation of endogenous auxins and cytokinins. For instance, exogenous IAA inhibits bush bud and shoot development in wheat by decreasing endogenous zeatin levels and increasing endogenous IAA in young shoot nodes. Conversely, under low nitrogen conditions, exogenous zeatin promotes the development of bush buds and shoots. Bud growth is positively correlated with endogenous zeatin levels but negatively correlated with the ratio of endogenous IAA: zeatin and ABA: zeatin. No significant correlations were observed between bud growth and the levels of endogenous IAA, gibberellins or ABA (Cai *et al*., 2018). Branching and tillering are critical processes for plant architecture and grain yield. Auxin and salicylic acid (SA) play antagonistic roles in the regulating tillering (Yuan *et al*., 2023). The gene *Less Tiller 1* (*LT1*) reduces auxin content by inhibiting *TrpA* and increases cytokinin levels by suppressing *TaCKX5s*, which encode cytokinin-degrading enzymes (Yuan *et al*., 2024). Cross-talk between auxin and other hormones - such as brassinosteroids, cytokinins, ethylene and gibberellins - affects the expression of genes responsible for leaf and root development in maize (Cowling *et al*., 2023). The balance between auxin and SA regulates primary root elongation and lateral root formation (Rivas *et al*., 2022), promotes internode elongation (Ren *et al*., 2023) and facilitates cell division and gibberellic acid production at the base of the developing maize leaves (De Vos *et al*., 2020). Ethylene modulates auxin-mediated gravitropic root movements in rice and maize by influencing auxin biosynthesis (Kong *et al*., 2024).

Changes in the expression of genes regulating auxin, brassinosteroids, jasmonic and gibberellic acids and ethylene biosynthesis, transport and signaling disrupt floral organ development, inhibit pollen formation and lead to unisexual flowers and male/female sterility in cereals (Smith & Zhao, 2016). Hormonal interactions among auxins, gibberellins, cytokinins and ABA in different parts of the barley ear (*Hordeum vulgare* L.) regulate the duration of development stages, floral atrophy and inflorescence development. Proper regulation of hormone levels during barley development is essential for determining flower location within the inflorescence, offering potential strategies to enhance grain yield (Boden, 2017; Youssef & Hansson, 2019). The interaction between IAA and cytokinins establishes reverse basal-apical hormone gradients during ear formation (Youssef *et al*., 2017; Zwirek *et al*., 2019). Basipetally transported IAA from the inflorescence to the internodes and nodes of barley is essential for the biosynthesis of gibberellins GA_1 and GA_3 in the stems (Wolbang *et al*., 2004). In rice, IAA regulates the expression of *OsIPT* (*adenosine phosphate isopentenyltransferase*) genes, thereby inhibiting cytokinin biosynthesis in tiller nodes and modulating tiller bud growth (Liu *et al*., 2011).

5. Endogenous auxins under stress

Climate change and environmental pollution are major threats to cereal crops productivity (Kosakivska *et al*., 2024a). Abiotic stresses induce morphological, anatomical, physiological, biochemical and molecular changes, adversely affecting photosynthesis, respiration, growth, reproduction and yield (Nadarajah *et al*., 2020; Ullah *et al*., 2022). In response to environmental challenges, plants have evolved complex defense mechanisms in which phytohormones play a pivotal role (Figure 5) (Kosakivska *et al*., 2022a; Ortiz-García *et al*., 2023; Swain *et al*., 2023; Waswani & Ranjan, 2023).

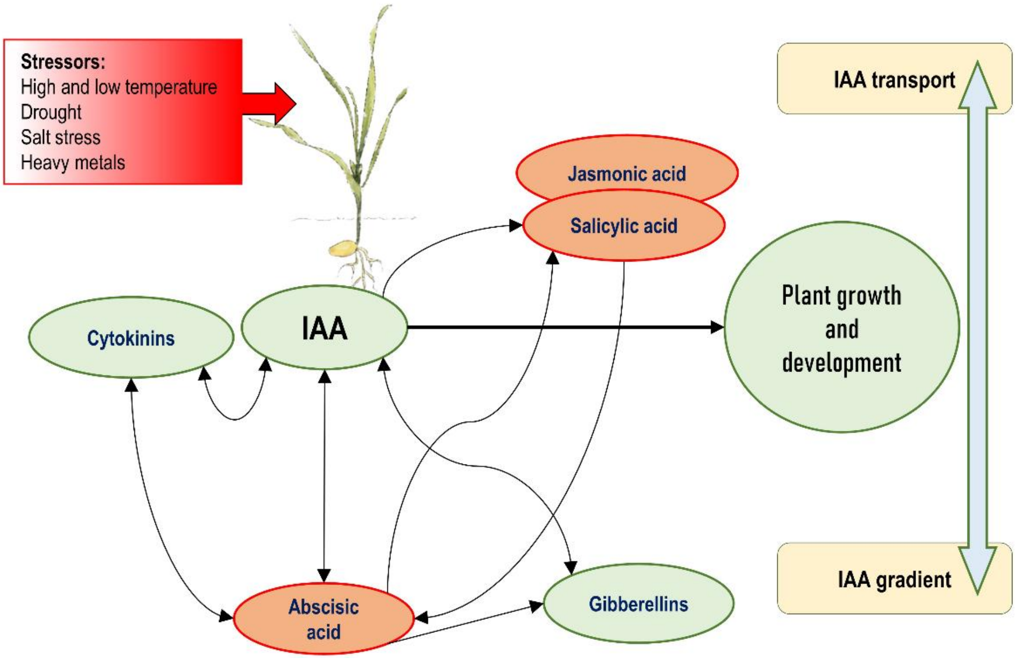

Figure 5. The crosstalk between auxins and other phytohormones regulates growth and development of cereals under abiotic stresses. The intracellular gradient of auxin, which is regulated by transporters, plays a central role in the regulation of hormonal interaction with other hormones and helps to resist stress by enhancing antioxidant protection, increasing photosynthetic activity, stabilizing membranes, inducing cell division, regulating stomatal activity, stimulating root growth, water uptake and nutrients

Under stress, the content of endogenous auxin decreases in most cereals. Studies on *Triticum aestivum* L. cv ‘Podolyanka’ and *Triticum spelta* L. cv. ‘Frankenkorn’ revealed that stress-induced growth changes in 14-day-old plants were accompanied by shifts in phytohormonal balance and localization within shoots and roots. The extent of IAA reduction during short-term heat stress (+40°C for 2 h), chilling stress (+4°C for 2 h) and moderate soil drought (4 days without irrigation) varied depending on the organ- and species-specific characteristics of the cereals. In wheat, roots were more sensitive to all stress types, whereas in spelt, shoots were more affected. Generally, IAA levels were lower in roots than in shoots, except for wheat roots under high temperature (Kosakivska *et al*., 2021; 2022b; Voytenko *et al*., 2024).

High temperatures significantly reduced auxin levels in rice spikelets, causing abnormal flower differentiation and spikelet degradation (Fu *et al*., 2015; Zhang *et al*., 2017, 2018). In wheat and barley anthers, high temperatures suppressed the expression of auxin biosynthesis genes (*YUCCA*), lowering auxin levels and hindering pollen development. In wheat cultivated under high temperatures and dry or semi-arid soil conditions, changes were observed in carbohydrates, proteins, proline and phytohormone levels in flag leaves and spikelets. With increasing temperature and decreasing soil moisture, IAA and gibberellin (GA_3) levels declined, while ABA increased. The impact of high temperature on plant growth and development was more pronounced than that of low moisture (Yasmeen, 2008).

Cold stress triggered similar hormonal changes in spring and winter wheat (*Triticum monococcum*), with dehydrins and phenolic acids accumulating during the adaptation phase to stabilize auxin levels and antioxidant functions (Vanková *et al*., 2014). During early cold exposure (+4°C), auxin levels in wheat leaves dropped significantly (Kosova *et al*., 2012). In ABA-deficient barley mutants, indole-3-butyric acid (IBA) levels increased under low temperature, whereas in wild-type barley (cv. Steptoe), IAA levels decreased significantly (Guo *et al*., 2023). In rice, auxin homeostasis influenced ABA biosynthesis and responses to abiotic stress (Ortiz-García *et al*., 2023). Carotenoid-deficient rice lines displayed enhanced cold tolerance due to reduced IAA levels, mitigated oxidative damage and improved membrane stability. Crosstalk between IAA and ABA at biosynthetic and developmental levels differentially impacted rice genotypes' drought and cold tolerance (Du *et al*., 2013a). Overexpression of the rice *OsGH3-2* gene, which encodes an enzyme conjugating IAA with amino acids and modulating ABA levels, induced drought oversensitivity. This overexpression led to dwarfing, reduced free IAA and ABA levels, larger stomatal apertures and faster water loss, despite enhanced cold tolerance in certain genotypes (Du *et al*., 2012). Cold tolerance in *Digitaria eriantha* (a cereal weed) was associated with chlorophyll and cytokinin stability, increased IAA levels and preservation of normal shoot and leaf structure (Garbero *et al*., 2012). In winter wheat, the levels of IAA, ABA and zeatin riboside (ZR) in leaves, roots and stem nodes under low temperatures correlated with the cold tolerance of the varieties. Cold-tolerant varieties showed more intense phytohormone accumulation and lower IAA:ZR ratios in stem nodes, contributing to increased tillering and cold resistance (Wang *et al*., 2009). In maize, auxin transporter genes (*ZmPIN*, *ZmPILS*, *ZmLAX* and *ZmABCB*) were highly expressed in shoots but repressed in roots under drought, salt and cold stress (Yue *et al*., 2015).

Overexpression of the *OsPIN3t* gene, which is involved in polar auxin transport, induced drought resistance in rice plants (Zhang *et al*., 2012). Similarly, the *OsIAA6* gene, a member of the Aux/IAA gene family, enhanced drought resistance and shoot growth in rice by regulating auxin biosynthesis (Jung *et al*., 2015). In sorghum, delayed leaf senescence or "stay-green", is a key factor in drought adaptation. Quantitative trait loci (QTL) associated with "stay-green" traits have been linked to genes encoding IAA amido synthetase, which inhibits IAA formation (Rama Reddy *et al*., 2014), as well as to *PIN* genes of the auxin efflux transporter family (Borrell *et al*., 2022; Wong *et al*., 2023). In maize, the expression of most auxin transporter genes (*ZmPIN, ZmPILS, ZmLAX* and *ZmABCB*) increased under drought, salt and cold stress (Yue *et al*., 2015). Overexpression of *ZmPIN1* enhanced IAA transport from the shoots to the roots, increased lateral root development and improved drought resistance (Li *et al*., 2018). In wheat, auxin accumulation in the root system reduced daily water use and modulated plant hydraulic properties, leading to increased yields under drought conditions (Sadok & Schoppach, 2019).

Rice plants are particularly sensitivity to drought and high temperature during reproductive development. Both stresses caused a reduction in endogenous IAA content and disrupted auxin signaling, resulting in spikelet sterility of rice s (Sharma *et al*., 2018). In winter wheat, under simulated drought or waterlogging from the fourth day after flowering to grain ripening, IAA levels changed depending on growth stage. During the grain filling and ripening phase, IAA levels in roots, leaves and grains significantly decreased. These hormonal changes coincided with reductions in starch and protein content in grains and overall yield. Stress-induced decreases in IAA, ZR and GA_{1+3} levels were accompanied by an increase in ABA (Xie *et al*., 2003). In 10-day-old wheat plants subjected to a 5-day drought, leaf length decreased, but root length remained unaffected. Stress caused no significant change in IAA levels across tissues; however, ABA, *cis*-zeatin and its riboside increased, while *trans*-zeatin, jasmonates, salicylic acid and gibberellins (GA_1 and GA_4) and their derivatives decreased (Ptošková *et al*., 2022). Reduced soil moisture led to a decline in IAA and GA levels in wheat leaves and spikelets, alongside increased proline and ABA accumulation (Bano & Yasmeen, 2010). In rice, drought reduced IAA level, whereas high and low temperatures increased its content (Du *et al*., 2013b). The accumulation of free IAA in maize roots was associated with the expression of *ZmGH3* genes, which were induced by salinity, drought and cadmium pollution and hormones like ABA, SA and JA (Feng *et al*., 2015).

Under salt stress, maize exhibited increased expression of auxin transporter genes *ZmPIN, ZmPILS, ZmLAX* and *ZmABCB* in shoots but decreased expression in roots (Yue *et al*., 2015). In wheat, salinity-induced germination delay and reduced germination energy were partially alleviated by soaking seeds in IAA and IBA solutions. The accumulation of dry weight in seedlings correlated with salinity level and hormone concentration (Gulnaz *et al*., 1999). In rice, NaCl stress significantly reduced IAA levels in leaves, but exogenous GA_3 application partially mitigated the adverse effects on growth and development (Prakash & Prathapasenan, 1990). Pretreatment of wheat with salicylic acid prevented reductions in IAA and cytokinin levels and maintained high ABA levels under salt and water deficit conditions. These changes facilitated quicker recovery and activation of stress-adaptation mechanisms (Sakhabutdinova *et al*., 2003). Exogenous salicylic acid treatment also reversed salinity-induced decreases in IAA content in maize plants (Fahad & Bano, 2012). Under oxygen deprivation, IAA levels increased in wheat and rice seedlings, with the highest accumulation observed in rice roots. Auxin levels returned to control values after stress cessation (Yemelyanov *et al*., 2020). Water immersion decreased total auxin levels in rice coleoptiles (Hoson *et al*., 1992).

Heavy metals (HMs) often reduce endogenous auxin levels in plants by altering hormone biosynthesis and signaling pathways (Moeen-ud-din *et al*., 2023). For example, cadmium (Cd) disrupted auxin homeostasis in barley roots. Under moderate Cd stress, auxin accumulates in root tips, but severe pollution reduces auxin levels, increases ROS production and halts root growth (Demecsová *et al*., 2020a; Zelinová *et al*., 2015). In *Sorghum bicolor* seedlings, Cd inhibited primary root growth, disrupted cell cycle in root tips, reduced IAA content and auxin hormone biosynthesis genes (Zhan *et al*., 2017). Similarly, Cd suppressed lateral root development in rice by rapidly decreasing the expression of auxin transporter genes (*OsPIN1b, OsPIN1c* and *OsPIN9*) (Wang *et al*., 2021). Cd and arsenic (As) stress impaired auxin biosynthesis and transport in *Oryza sativa* roots by altering the expression of biosynthesis genes (*ASA2* and *YUCCA2*) and transporter genes (*AUX1* and *PIN5b*), which inhibited growth and reduced productivity (Ronzan *et al*., 2018). Cd stress also disrupted mitogen-activated protein kinase (MAPK) signaling, leading to growth inhibition and impaired root elongation due to disturbed auxin homeostasis. The MAPK signaling pathway negatively regulated key auxin signaling genes (*OsYUCCA*, *OsPIN*, *OsARF* and *OsIAA*) and cycle-related genes (Zhao *et al*., 2013a). However, the auxin transporter OsAUX1 played a crucial role in primary root and root hair elongation in rice, enhancing resistance to Cd stress (Yu *et al*., 2015). In maize, aluminum (Al) stress suppressed auxin accumulation and inhibited root growth (Zhang *et al*., 2019). In hydroponically grown wheat, Al stress increased IAA accumulation in root tips at higher Al concentrations (25, 50, 100 μM) while reducing IAA oxidase activity. The TIR1/AFB auxin signaling pathways have been implicated in the regulation of barley root growth under aluminum stress (Bai *et al*., 2017). A strong positive correlation ($R^2 = 0.9859^*$) was observed between malic acid efflux rates and endogenous IAA levels, indicating IAA's involvement in Al-induced malic acid efflux (Yang *et al*., 2011). The TIR1/AFB auxin signaling pathway was also implicated in regulating barley root growth under Al stress (Bai *et al*., 2017). Overexpression of the auxin transporter gene *OsPIN2* in rice reduced Al-induced ROS formation, lipid peroxidation and lignification in roots, while enhancing basipetal auxin transport inhibition. This increased IAA content, proton release and resistance to Al stress (Wu *et al*., 2014). Short-term Al exposure (90 μM Al at pH 4.5 for 1 h) in maize caused auxin accumulation in the root tips, while hormone concentrations in the elongation zone decrease due to inhibited basipetal transport (Kollmeier *et al*., 2000). Roots sensitivity to Al stress depended on localized auxin changes driven by reduced acropetal transport. The auxin importer OsAUX3, involved in acropetal hormone transport, accumulated in the root tips of rice under Al stress, further inhibiting root growth (Wang *et al*., 2019). Inoculation of wheat with *Penicillium ruqueforti* Thom., an IAA-producing funfus, improved plant resistance to nickel (Ni), Cd, copper (Cu), zinc (Zn) and lead (Pb) (Ikram *et al*., 2018). Zinc at a concentration of 228 mg/L inhibited winter wheat root growth, decreased the levels of endogenous IAA, ABA and zeatin, while increasing gibberellins, isopentenyladenosine and SA. Adding 10^{-6} M ABA to the incubation medium enhanced root growth and increased the content of the stress-related hormones ABA and SA (Kosakivska *et al*., 2019; Voytenko *et al*., 2019).

6. Exogenous auxins in the regulation of stress resistance

Exogenous application of plant growth regulators has emerged as an alternative strategy to enhance abiotic stress resistance in plants (Kosakivska *et al*., 2022a). Exogenous IAA improved drought resistance in wheat by enhancing antioxidant activity, increasing carbohydrate and protein content and promoting biomass accumulation (Muhammad *et al*., 2016). In rice, exogenous IAA reduced lipid peroxidation and ROS accumulation in spikelets under drought and high-temperature stress (Sharma *et al*., 2018). Priming wheat grains with tryptophan and IAA solutions under soil salinity conditions improved germination efficiency by increasing SA levels in leaves (Iqbal & Ashraf, 2007). Enhanced germination and plant growth from tryptophan-primed grains were associated with reduced Na^+ uptake by roots, limited translocation to shoots and improved Ca^{2+} distribution in roots. Although exogenous IAA did not affect radicle length, it increased hypocotyl length, fresh and dry weight accumulation in seedlings and dry weight of wheat hypocotyls under salinity stress (Akbari *et al*., 2007). Foliar application of naphthaleneacetic acid (NAA) enhanced catalase activity, increased spikelet numbers and improved wheat yield on saline soils (Khedr *et al*., 2022). Similarly, foliar spraying of *Zea mays* L. leaves with IAA, combined with soil application of potassium (K) and phosphorus (P) as monopotassium phosphate at sowing, mitigated salt stress. This synergistic treatment improved ion redistribution in plant tissues, stimulated growth, increased photosynthetic pigment concentrations, reduced membrane permeability and enhanced the activity of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (Kaya *et al*., 2013). Under salt stress, exogenous IAA and kinetin improved grain yield of *Oryza sativa L*. by increasing the content of starch, sucrose, glucose and fructose. The combination of these hormones contributed to an increase in the content of endogenous IAA in the grain and also stimulated cell division, stretching and expansion (Javid *et al*., 2011). Exogenous IAA promoted the resistance of wheat plants under anoxia by reducing electrolyte leakage, ROS production and lipid peroxidation (Yemelyanov *et al*., 2020). In *Oryza sativa* L., a combination of exogenous IAA and kinetin under salt stress increased grain yield by boosting starch, sucrose, glucose and fructose levels. These hormones also enhanced endogenous IAA content in grains, stimulated cell division and promoted cell elongation and expansion (Javid *et al*., 2011). Moreover, exogenous IAA improved wheat resilience under anoxic conditions by reducing electrolyte leakage, ROS production and lipid peroxidation (Yemelyanov *et al*., 2020).

Exogenous application of auxins and their precursors has been shown to enhance rice resistance to heavy metal toxicity by upregulating genes associated with auxin biosynthesis (Bilal *et al*., 2023). Priming *Triticum aestivum* grains with IAA solution (500 μM) improved cadmium (Cd) resistance (500–1000 μM) in 56-day-old plants, restoring growth, increasing photosynthetic pigment and relative water content, altering leaf anatomy and enhancing antioxidant activity to mitigate oxidative damage (Agami & Mohamed, 2013). Auxin transport inhibitors, such as 1-naphthoxyacetic acid (1-NOA) and 1-naphthylphthalamic acid (NPA), significantly reduced the resistance of *Sorghum bicolor* to Cd, whereas applying 1-naphthaleneacetic acid (NAA) improved resistance (Zhan *et al*., 2017). IAA reduced aluminum (Al) toxicity in wheat root tips by increasing rhizosphere pH through decreased plasma membrane H+-ATPase activity, while auxin transport inhibitors suppressed this effect (Wang *et al*., 2013). IAA also mitigated Al-induced inhibition of root elongation in maize (90 μM Al at pH 4.5) (Kollmeier *et al*., 2000) and facilitated malic acid efflux from wheat roots via anion channel activation during Al stress (Yang *et al*., 2011). Short-term treatment (2 hours) of rice seedling roots with L-tryptophan solutions increased plant height, panicle number, grain weight and yield in Cd-contaminated soil. Stabilizing endogenous IAA levels promoted Cd accumulation in straw while reducing its concentration in grains (Farooq *et al*., 2015). Exogenous IAA application under NaCl and Pb stress enhanced shoot and root growth, biomass, photosynthetic pigment levels, phenolic compounds and flavonoids in maize (Aizaz *et al*., 2023). IBA mitigated Cd toxicity in maize roots, enhancing mineral uptake and growth (Šípošová *et al*., 2021). It improved Cd fixation on cell walls, increased endogenous IAA levels, reduced lignin content, increased Ca^{2+} and phenol levels and altered monosaccharide composition (Šípošová *et al*., 2023). Foliar treatment of ryegrass (*Lolium perenne* L.) with IAA improved resistance to Pb toxicity by increasing biomass, photosynthetic pigment content and antioxidant activity (Zhu *et al*., 2023). IAA pretreatment reduced arsenic toxicity in rice seedlings by promoting root and shoot growth and lowering arsenic levels in grains (He *et al.*, 2022). Combining exogenous auxin (3 μM) with selenium (20 μM) alleviated arsenic stress, improving seedling growth, chlorophyll content, protein levels and antioxidant compounds such as cysteine, proline, and malondialdehyde (Pandey & Gupta, 2015). Under arsenic contamination, silicon (Si) induced accessory root formation in rice by upregulating nitric oxide metabolism genes (*OsNOA1*), cell cycle regulators (*OsCDKA1*), IAA biosynthesis genes (*OsYUCCA1*, *OsTAA1*), auxin transporters *(OsPIN1*, *OsPIN5*, *OsPIN10*) and Si uptake genes (*OsLsi1*, *OsLsi2*). However, polar auxin transport inhibitors like TIBA suppressed root formation despite the presence of Si and nitric oxide donors (Tripathi *et al.*, 2021). Exogenous IBA alleviated Cd toxicity in barley root tips by inducing NO production and increasing glutathione peroxidase activity, protecting plants from oxidative stress (Demecsová *et al.*, 2020b). Cadmium reduced NO levels, increased H_2O_2 accumulation and disrupted auxin distribution in rice roots. However, exogenous IAA and IBA mitigated these effects by enhancing lateral root growth and NO content (Piacentini *et al.*, 2020). Exogenous sodium nitroprusside improved rice seedling resistance to mercury (Hg) by altering IAA transport in roots, promoting root growth (Chen *et al.*, 2015). Conversely, under iron deficiency, NO inhibited root elongation by reducing auxin levels (Sun *et al.*, 2017). The combined use of NO and auxins under HM stress shows mixed outcomes. While NO can enhance resistance, it may also limit auxin transport, affecting root formation and growth (Demecsova & Tama ́s, 2019; Ganguly *et al.*, 2022).

7. Conclusion

Discovered over a century ago, auxin is a key hormone regulating plant growth and development, playing a crucial role in integrating abiotic stress signals and orchestrating subsequent stress responses. Auxin is synthesized in the shoot apex, root tips and rapidly growing tissues and organs. Its biosynthesis, metabolism and signaling pathways define its role in regulating growth, development and stress response formation. Auxin acts as a mediator in perceiving and transmitting environmental signals, interacting with other phytohormones to regulate plant growth and maintain cellular homeostasis. Exogenous auxins and synthetic hormone analogs have practical applications in agriculture, enhancing crop yield and quality. Further research on auxin’s role in stress resistance, particularly in cereal crops, will advance biotechnological strategies for exogenous hormone application. This can help improve plant growth and productivity under adverse environmental conditions, contributing to sustainable agricultural practices.

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