Cereals and Phytohormones Under Drought Stress

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Abstract

Climate change is expected to amplify drought frequency and intensity, with a significant alteration of the ecosystems. It affects the livelihoods, communities, and productivity of many important crops globally, including cereals. These crops are vulnerable to drought stress due to disturbed growth, nutrient acquisition, and cell functioning and biochemistry, which decrease yields and grain quality. Thus, understanding plants' drought stress tolerance mechanisms could be an effective strategy for ensuring continuous productivity.

Drought stresses plants and associated factors (e.g. soil microorganisms), inducing adjusted responses involving plant-soil signalling via phytohormones. The coordination of plant responses to drought by phytohormones is of great interest owing to the plants' sessility, and their subsistence relies mainly on their aptitude to quickly regulate their growth and physiology processes and to alleviate drought stress effects. Phytohormones are typically involved in these processes. Research interest has recently been focused on understanding phytohormones' multiple functions that are critical regulators of plant functioning, including cell expansion and division, endogenous level of metabolites, and gene expression. Phytohormones, especially abscisic acid (ABA), salicylic acid (SA), jasmonate (JA), ethylene (ET), auxin (IAA), cytokinins (CKs), brassinosteroids (BRs), gibberellins (GAs), and strigolactones (SLs) are known to be involved in plants' tolerance to drought. Some reduce water loss through regulating stomata opening, while others induce root development, accumulation of osmolytes, and antioxidant enzymes to protect plant cells from stress-related damages. Some of these signalling molecules could be either produced by plants suffering from water deficiency or induced by the presence of microorganisms. Besides, they could also be exogenously applied to vegetative tissues and soil. Despite several studies on phytohormone effects, their mechanisms and possible crosstalk are still a subject of debate. Thus, this chapter presents an overview of the different roles of phytohormones in regulating cereals' adaptive responses to drought stress severity and the potential factors to alter their effectiveness in mitigating this constraint in cereals.

Keywords

Drought stress · Phytohormones · Cereal crops · Tolerance · Signalling pathways

Abbreviations

13-LOX	13-Lipoxygenase
9'-c-n	9'-Cis-neoaxanthin
α-LeA	α-Linolenic acid
AAO	ABA Aldehyde oxidase
ABA	Abscisic acid

ACC	1-aminocyclopropane-1-carboxylic acid
ACO	1-aminocyclopropane-1-carboxylic acid oxidase
ACS	1-aminocyclopropane-1-carboxylic acid synthase
AMF	Arbuscular mycorrhizal fungi
AOC	Allene oxide cyclase
AOS	Allene oxide synthase
APX	Ascorbate peroxidase
BA	Benzyladenine
BR	Brassinosteroid-Insensitive receptor
BRs	Brassinosteroids
CAT	Catalase
CCD	Carotenoid cleavage dioxygenase
CDK	Cyclin-dependent kinase
CDPK	Calcium-dependent protein kinase
Ch	Chitosan
CKs	Cytokinins
CKX	Cytokinin oxidase/dehydrogenase
CP	Cytochrome P450
CPKs/CDPKs	Calcium-dependent protein kinase
CPS	Copalyl diphosphate synthase
DMAPP	Dimethylallyl pyrophosphate
DREB/CBF	Dehydration-Responsive Element Binding proteins/C-repeat Binding Factor
EDS	Enhanced disease susceptibility
EIL	Ethylene insensitive-like protein
EL	Electrolyte leakage
EPS	Exopolysaccharides
EPS1	Enhanced *Pseudomonas* susceptibility 1
ERF	Ethylene response factor
ET	Ethylene
ETR	Ethylene receptor
F_v/F_m	Photosystem II efficiency
GA2ox	Gibberellin 2-oxidases
GAs	Gibberellins
GB	Glycine betaine
GPX	Glutathione peroxidase
GR	Glutathione reductase
GST	Glutathione S-transferase
HSP	Heat shock proteins
IAA	Indole-3-Acetic acid
IC	Isochorismate
ICS	Isochorismate synthase
iP	N^6-(Δ^2-isopentenyl)-adenine
IPA	Indole-3-pyruvate
IPT	Isopentenyl transferase

JA	Jasmonic acid
JA-Ile	Jasmonoyl isoleucine
JAZ	Jasmonate ZIM-domain
JIH	Jasmonoyl-l-isoleucine hydrolase
JMT	Jasmonic acid carboxyl methyltransferase
LEA	Late embryogenesis abundant
MAPKKK/MPK	Mitogen-activated protein kinase
MDA	Malondialdehyde
MeJA	Methyl jasmonate
MJE	Methyl jasmonate esterase
NCED	9-cis-epoxycarotenoid dioxygenase
NCEI	Neoxanthin synthase
NPR	Non-expressor of pathogenesis-related gene
NSY	Neoxanthin synthase
NXS	Neoxanthin synthase
OPDA	(cis)-12-oxophytodienoic acid
OPR	12-oxophytodienoate reductase
PAL	Phenylalanine ammonia-lyase
PEG	Polyethylene glycol
PGPF	Plant growth-promoting fungi
PGPR	Plant growth-promoting rhizobacteria
POD	Peroxidase
PP2C	2C protein phosphatase
ROS	Reactive oxygen species
SA	Salicylic acid
SDR	Short-chain dehydrogenase/reductase-like
SLs	Strigolactones
SOD	Superoxide dismutase
SWE	Seaweed extract
TAA	Tryptophan aminotransferase of *Arabidopsis*
TF	Transcription factor
Trp	Tryptophan
tz	Trans-zeatin
WUE	Water use efficiency
ZEP	Zeaxanthin epoxidase enzyme

13.1 Phytohormones: Key Mediators of Cereal Responses to Drought Stress

Alarming environmental challenges have mounted and become more evident due to exacerbating water scarcity, industrialization, and extreme weather events. According to FAO (2018), up to 60% of the global population will suffer from water deficiency by 2025. Drought has recently received great importance since it is among the critical constraints that control and reduce the agricultural production of global crops (Iqbal et al. 2020; Meza et al. 2020). This constraint results in wide morphological, biochemical, and genetic disturbances and changes in plants and subsequently affects development, productivity, and yield (Ullah et al. 2018a; Boutasknit et al. 2021; Lahbouki et al. 2022). Thus, the impact of droughts threatens complex global food security and may reduce agricultural yields, including cereals (up to 10% decrease) (Lesk et al. 2016; Fu et al. 2021). To address this global issue, research in agriculture has targeted improving genetic resources and agricultural practices to enhance water use efficiency (WUE) (Haile et al. 2020; Ahluwalia et al. 2021). Additionally, this worrying scenario requires the urgent implementation of sustainable measures to improve crop yield and quality. Increasing attention has been focused on applying beneficial biostimulants to minimize the effect of drought.

Cereal crops, mainly rice, wheat, maize, sorghum, barley, and pearl millet provide more than 50% of the population's caloric requirements, particularly in developing countries in South Asia, sub-Saharan Africa, and Latin America (Olugbire et al. 2021). Cereal crops are known as an excellent source of total calories (48%) and total protein (42%) that contribute to more than two-thirds of dietary energy intake worldwide (Curiel et al. 2020). Cereals have been considered staple foods for most human populations for about 10,000 years due to specific characteristics such as ease of growth, development, storage, and transport (Wendin et al. 2020). In addition, cereals are classified as essential materials for producing animal feed and biofuels (Olugbire et al. 2021). However, cereal crops have experienced yield losses of up to 40% globally in wheat and maize caused by drought stress effects (Daryanto et al. 2016; Fu et al. 2021). Cereals are mostly grown in (semi-) arid areas and are often exposed to intense and prolonged drought episodes. Hence, understanding drought-responsive mechanisms in cereals and molecular signalling pathways is a time-demanding task.

Phytohormones are considered regulators of plant growth and development since they act through several pathways such as additive, synergistic, or antagonistic pathways to enhance growth under normal and stressful conditions (Sadiq et al. 2020; Li et al. 2021). These molecules also develop potential phenological and biochemical processes to keep the cells' relative water content (RWC) and water potential constant (Yadav et al. 2021). In response to drought stress conditions, several processes are elaborated by various phytohormones, such as abscisic acid (ABA), which plays a significant role in stomatal behaviour by responding to water deficiency (Li et al. 2021). Other phytohormones intervene in coordinating plant responses under drought conditions to different degrees, namely, salicylic acid (SA), jasmonic acid (JA), ethylene (ET), auxins (IAA), cytokinins (CKs), brassinosteroids (BRs), gibberellins (GAs), and strigolactones (SLs) (Tardieu et al. 2018; Ilyas et al. 2021; Yadav et al. 2021). These molecules act as chemical regulators of plant responses to multiple environmental stresses. Once the perception of the stress signal is established, a series of chemical reactions are released and activated in a network of interactions to enhance specific protective mechanisms, including stomatal closure, osmolyte accumulation, and antioxidant defense, in an attempt to escape water deficiency (Gupta et al. 2020; Yadav et al. 2021).

13.2 Correlations Between Phytohormones and Drought Stress Tolerance in Cereals

Phytohormones have essential roles in controlling multiple plants' acclimatization processes in response to water deficiency. ABA is the primary hormone that strengthens plant water stress tolerance via many processes such as stomatal movements, root expansion, and stimulation of ABA-dependent pathways (Cardoso et al. 2020; Nawaz and Wang 2020; Wang et al. 2021a). Additionally, JA, SA, ET, IAA, GAs, CKs, SLs, and BRs are also necessary to meet the challenges of water deficiency. These molecules commonly are in cross-talk to ensure plant survivability under drought stress (Ullah et al. 2018a). Various investigations have highlighted the impact of water stress on phytohormones and vice versa, usually concluding that there is a high correlation between drought stress and phytohormone production. For instance, Bano et al. (2012) compared the effects of ABA and drought stress application at pre-sowing and 55 days after sowing in two drought tolerance contrasting wheat varieties. The drought-resistant variety developed a great defense mechanism to mitigate reactive oxygen species (ROS) effects through stimulation of the antioxidant enzyme activity. Under water deficiency, ABA induced a significant increase in superoxide dismutase (SOD) and peroxidase (POD) activity, with a significant decrease in this activity in re-watering. For both wheat cultivars, ABA treatment significantly enhanced RWC under drought conditions. Furthermore, the sensitive variety was more responsive to ABA treatment and showed low concentrations of endogenic ABA.

On the other hand, the tolerant cultivar presented a great recovery from water stress at re-watering. In addition, the grain weight was significantly improved by ABA treatment for tolerant cultivars under water deficiency (Nayyar and Walia 2003; Bano et al. 2012). Drought stress decreased GA and IAA and increased ABA and proline in two wheat cultivars (Bano and Yasmeen 2010). ABA and benzyladenine (BA) application at the anthesis stage induced osmoregulation by proline production. BA was more effective at the early stages of grain filling, while ABA was more effective at the later stages (Bano and Yasmeen 2010).

Similarly, leaf GA and IAA content significantly decreased under drought stress (Xie et al. 2003). The correlation analyses between yields, starch, and protein content in grains and levels and ratios of four hormones indicated that the changes were associated with IAA and GA reduction and ABA increase, especially in grains. The overall results of these studies suggested that the varying concentrations of endogenic hormones under post-anthesis drought conditions could alter grain starch and protein content by regulating the activity and processes of the enzyme, which might be attributed to synthesis decrease (Xie et al. 2004) or a degradation decrease (Davenport et al. 1980) of IAA and GA. Foliar application of glycine betaine (GB) improved drought tolerance and yield of maize and sorghum, but not wheat

(Agboma et al. 1997). In contrast, drought significantly decreased maize and sorghum's grain numbers and yields. Foliar application of GB minimally enhanced biomass production in the three crops and significantly increased maize ($P = 0.001$) and sorghum ($P = 0.003$) grain yield.

13.3 Hormones' Signalling for Drought Stress Response and Tolerance

The evolution has enabled plants to develop multiple strategies to manage water scarcity. They have established mechanisms, including altered molecular, biochemical, and physiological processes (Bhargava and Sawant 2013; Seleiman et al. 2021). Such response mechanisms occur via plant hormone signalling pathways (Ilyas et al. 2021). Phytohormones are indispensable molecules that participate in various biological processes. Besides, they are vital to stress signalling pathways. The abiotic stress signalling in plants depends on the nature, intensity, and length of exposure.

In the signalling cascade, phytohormones are instrumental in orchestrating plant development, growth, and tolerance mechanisms (Tiwari et al. 2017; Tardieu et al. 2018; Jogawat et al. 2021).

Here, we will focus on the signalling pathways related to each of the nine hormones involved in drought tolerance in cereals.

13.3.1 Abscisic Acid (ABA)

ABA is a sesquiterpenoid phytohormone often labelled as "stress hormone" due to its discrete association with plant abiotic stress mitigation (Zhao et al. 2021). Therefore, this molecule is the hormone of abscission and is probably the most studied of plant hormones (Chen et al. 2021b). ABA is formed via the carotenoid pathway (Fig. 13.1). Zeaxanthin is transformed to all-trans-violaxanthin by antheraxanthin. This reaction is activated by the zeaxanthin epoxidase enzyme (ZEP; EC 1.14.13.90) (Agrawal et al. 2001), followed by the conversion of trans-violaxanthin to 9-cis-violaxanthin and 9-cis-neoxanthin. Neoxanthin synthase (NXS; EC 5.3.99.9) is involved in these reactions (North et al. 2007). The final reaction to ABA production takes place in chloroplasts and is catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED; EC 1.13.11.51) (Iuchi et al. 2001). The first-ever NCED gene was studied in the maize *vp14* mutant and is activated under water deficiency in the course of seed maturation (Tan et al. 1997). ABA orchesters diverse physiological functions and developmental phases, such as seed development and dormancy (Sano and Marion-Poll 2021), stomatal opening (Hasan et al. 2021), embryo morphogenesis (Kruglova et al. 2021), and biosynthesis of storage lipids and proteins (Ali et al. 2022). Furthermore, ABA is also implicated in controlling the expression of genes implicated in the ABA signalling pathways (Some et al. 2021). The role of ABA as a crucial messenger in mitigating stress

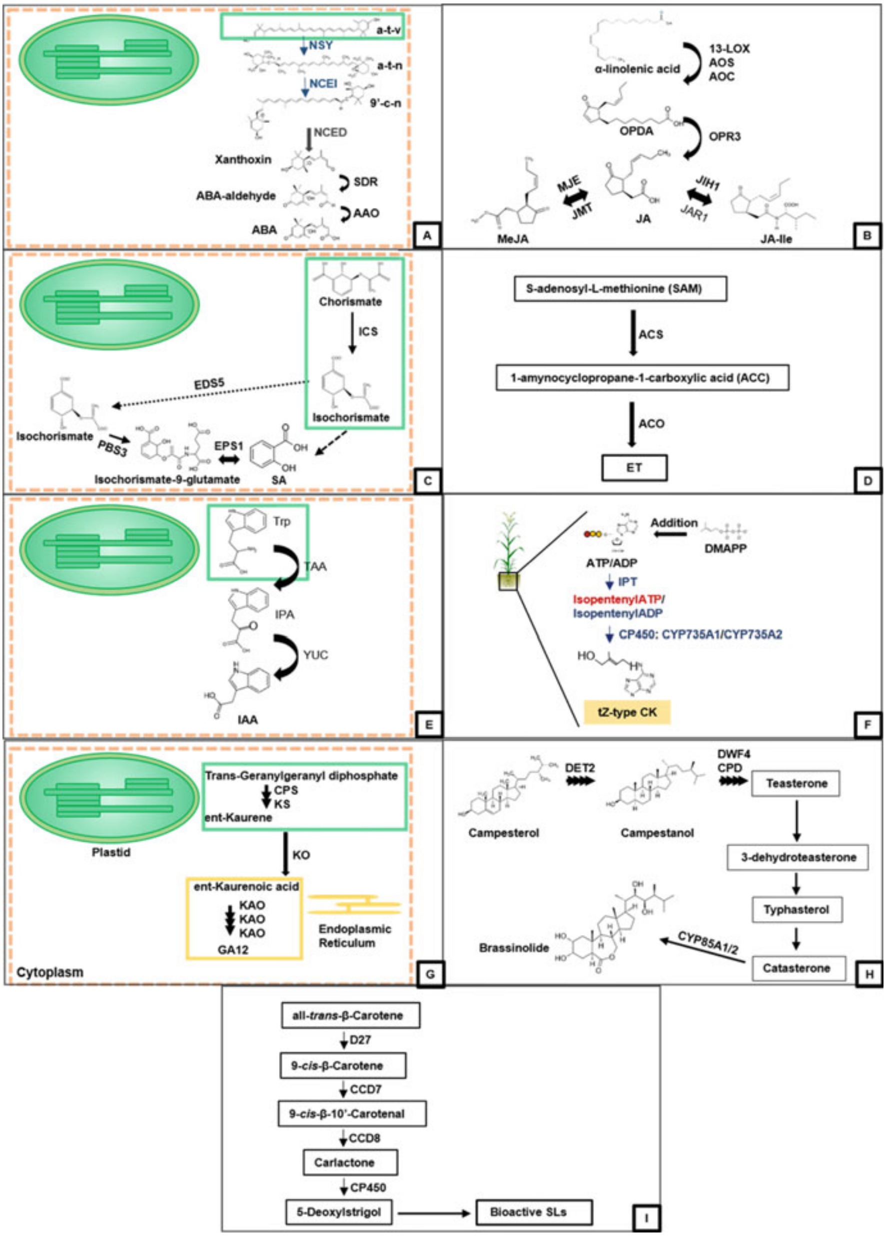

Fig. 13.1 Schematic diagrams of the major plant hormone generation and signalling pathways. (**a**) Abscisic acid, (**b**) jasmonates, (**c**) salicylic acid, (**d**) ethylene, (**e**) indole-3-acetic acid, (**f**) cytokinins, (**g**) gibberellins, (**h**) brassinosteroids, and (**i**) strigolactones. *13-LOX* 13-lipoxygenase, *9'-c-n* 9'--cis-neoaxanthin, *AAO* ABA aldehyde oxidase, *ACO* 1-aminocyclopropane-1-carboxylic acid oxidase, *ACS* 1-aminocyclopropane-1-carboxylic acid synthase, *AOC* allene oxide cyclase, *AOS* allene oxide synthase, *a-t-n* all-trans-neoxanthin, *a-t-v* all-trans-violaxanthin, *CCD* carotenoid cleavage dioxygenase, *CP450* cytochrome P450, *CPS* copalyl diphosphate synthase, *D27* dwarf27, *DET2 DEETIOLATED2* gene, *DMAPP* dimethylallyl pyrophosphate, *DWF4* dwarf4, *EDS5* enhanced

and improving plant tolerance has received much attention (Wilkinson and Davies 2002). To cope with drought stress, cellular ABA content tends to rise, leading to the plant hormone binding to the receptors of pyrabactin resistance (PYR/PYL/RCARs), which inactivates type 2C protein phosphatases (PP2Cs) (Siodmak and Hirt 2021). The protein kinases, SnRK2s, are auto-stimulated after dissociation from PP2Cs, which triggers ABA responses. In addition, calcium-dependent protein kinases (CDPKs) play a role in ABA signalling. CDPKs were described in rice (29 CDPKs), wheat (20), and maize (35) (Schulz et al. 2013). Under drought stress, implicated signalling pathways and gene expression levels (more than 10% of protein-encoding genes) are de-regulated in response to increased endogenous ABA levels (Nemhauser et al. 2006; Canales et al. 2021), which results in limiting water loss through the reduction of leaf expansion and stomatal opening (Wilkinson et al. 2012). Another attribute to ABA resides in its implication in robustness and development of root architecture (Wilkinson et al. 2012; Benderradji et al. 2021). In addition, ABA interferes in synthesizing dehydrins and Late Embryogenesis Abundant (LEA) proteins (Sun et al. 2021). Tolerance is indeed conferred on plants owing to the upregulation by ABA of production of osmoprotectants, maintenance of cell turgor, and stimulation of antioxidant defense (Chaves et al. 2003). In a study conducted by Dominguez and Carrari (2015) on drought-tolerant Zhengdan 958 and drought-sensitive Xundan 20 maize hybrids, exogenous S-ABA helped mitigate drought stress by enhancing *Asr1* (ABA, stress, ripening) gene expression levels.

13.3.2 Jasmonates (JAs)

JAs are a group of hormones formed by cyclopentanone that include free jasmonic acid (JA) (the most common form) and methyl jasmonate (MeJA) (Fig. 13.1). These plant hormones are very abundant across different plant species. JAs are crucial for plant development and survival. They are required for senescence, flowering, fruiting, direct and indirect defense responses, and secondary metabolism (Wu et al. 2008; Fahad et al. 2015). JAs are synthesised from α-linolenic acid (α-LeA) through the galactolipase (Li et al. 2021a). JA formation is initiated by oxygenation of 13-lipoxygenase, the 13(S)-hydroperoxy-octadecatrienoic acid is transformed to an epoxide by a 13-allene oxide synthase and cyclized to the

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Fig. 13.1 (continued) disease susceptibility 5, *EPS1* enhanced *pseudomonas* susceptibility 1, *ICS* isochorismate synthase, *IPA* indole-3-pyruvate, *IPT* isopentenyl transferase, *JA-Ile* jasmonoyl isoleucine, *JIH1* jasmonoyl-l-isoleucine hydrolase 1, *JMT* jasmonic acid carboxyl methyltransferase, *KAO* ent-kaurenoic acid oxidase, *KS* ent-kaurene synthase, *MeJA* methyl jasmonate, *MJE* methyl jasmonate esterase, *NCED* 9-cis-epoxycarotenoid dioxygenase, *NCEI* neoxanthin synthase, *NSY* neoxanthin synthase, *OPDA* cis-oxo-phytodienoic acid, *OPR3* 12-oxophytodienoate reductase 3, *PBS5* phosphate-buffered saline 5, *SDR* short-chain dehydrogenase/reductase-like, *TAA* tryptophan aminotransferase of *Arabidopsis*, *Trp* tryptophan, *tz* trans-zeatin cyclopentenone (cis)-12-oxophytodienoic acid (OPDA) by an allene oxide cyclase. In this step, the enantiomeric structure of the naturally occurring (þ)-7-iso-JA ((3R,7S)-JA) is established (Wasternack et al. 2013). JAs act as a plant defense activator when subjected to abiotic stresses, including drought (Pauwels et al. 2009; Seo et al. 2011). JA ZIM-domain (JAZ) proteins play a significant role in the JA signalling pathway. JAI3/JAZ proteins bind to transcription factors (TFs) under normal conditions. Under stress conditions, however, JA and its derivatives accumulate, and JAZ proteins degrade, leading to the activation of TFs, which upregulate the genes implicated in stress responses (Liu et al. 2017; Han and Luthe 2021). Furthermore, JA induces the development of roots and ROS scavenging and the closure of stomata via the JA precursor, OPDA (Wang et al. 2021b). Allagulova et al. (2020) indicated that dehydrins might participate in the methyl jasmonate (MeJA)-induced protecting effect in wheat plants subjected to drought stress. Treated plants with 0.1 μM of exogenous MeJA decreased membrane structure lesions. Furthermore, TADHN dehydrin transcripts and dehydrin protein expression increased during dehydration.

13.3.3 Salicylic Acid (SA)

SA is a naturally occurring phenolic compound implicated in pathogenesis-associated protein expressions (Chen et al. 2012). It plays a crucial role in regulating plant growth (Bernal-Vicente et al. 2018), ripening and development (Changwal et al. 2021), and in triggering plants' responses to abiotic stresses; including drought (Miura et al. 2013), salt (Khodary 2004), and heat (Fayez and Bazaid 2014). Two routes are involved in the biosynthesis of SA: the isochorismate (IC) and the phenylalanine ammonia-lyase (PAL) pathways, with the IC pathway being the major one (Fig. 13.1) (Uppalapati et al. 2007). While low concentrations of SA can increase the antioxidant machinery, high concentrations can lead to cell death and vulnerability under abiotic constraints (Prakash et al. 2021). SA triggers the expression of genes encoding chaperones, heat shock proteins (HSP), antioxidants, and genes involved in the biosynthesis of cytochrome P450 and secondary metabolites, sinapyl alcohol dehydrogenase, and cinnamyl alcohol dehydrogenase (Jumali et al. 2011).

SA responses to the environment occur through the nonexpressor of pathogenesis-related genes, *NPR1*, expressing *PR* genes (Maier et al. 2011). Activated genes like *WRKYs* and *TGAs* improve plants' tolerance against biotic and abiotic stresses (Chen et al. 2012; Ullah et al. 2018b). SA content in barley roots was enhanced ca. 2x under water stress (Bandurska 2005). SA-inducible pathogenesis-related genes *PR1* and *PR2* were incited in response to water deficits (Miura et al. 2013). NPR1 protein acts as a regulator of the SA-controlled signalling pathway, especially under pathogen infection. SA accumulation implicates antimicrobial NPR1 proteins in the defense process, leading to the import of monomeric NPR1 to the nucleus, where it binds with SA and generates a conformational change that conducts to the C-terminal activation domain that triggers transcription. Another work on two wheat varieties, drought-tolerant Kundan and drought-sensitive Lok1, subjected to 75 and 50% reduction of RWC and recovery, revealed that SA-induced thioredoxins activated defense responses against ROS, leading to drought tolerance (Sharma et al. 2017).

13.3.4 Ethylene (ET)

ET constitutes a simple hydrocarbon gaseous molecule that acts as a plant hormone. ET is implicated in specific stages of plant growth and development, particularly fruit ripening (Liu et al. 2021), flower senescence (Naing et al. 2021) and the abscission of petals and leaves (Yang et al. 2021). The primary precursor of ET is 1-aminocyclopropane-1-carboxylic acid (ACC) (Fig. 13.1). ACC synthase is the enzyme that catalyzes the conversion of *S*-adenosyl-L-methionine to ACC, which is later converted to ET by the action of ACC oxidase (Bleecker and Kende 2000). One of the prominent roles of ET is the regulation of drought tolerance in plants. APETELA2/Ethylene-Responsive Element-Binding Protein (AP2/EREBP) genes have been found to respond to drought (Dong et al. 2021). The expression of *GmERF3*, an ethylene response factor (ERF), was shown to be induced under drought and salt stresses, conferring tolerance to plants (Zhang et al. 2009; Ilyas et al. 2021). Another ERF gene, *AtERF019*, acted positively in delaying senescence (Scarpeci et al. 2017), whereas transgenic plants have shown improved tolerance to drought by lowering transpiration rate and regulating stomatal regulation aperture and cuticle-thinning.

Environmental stress leads to ET accumulation, which improves the survival of plants under adverse environmental conditions (Gamalero and Glick 2012; Salazar et al. 2015). *SUB1A*, an ethylene-response-factor-like gene and an ETS2 Receptor Factor present in limited rice accessions, attributed submergence tolerance to rice (Xu et al. 2006; Fukao et al. 2011). Genotypes with the *SUB1A* gene could recover after desubmergence via the establishment of new leaves (Fukao et al. 2006). These findings suggest that *SUB1A* also may help the process of enduring several abiotic stresses. Under drought stress, *EIN2* downstream signalling components are kept inactive by the action of a Raf-like kinase and critical negative regulator of ET, *CTR1* kinase-dependent phosphorylation (Eppel and Rachmilevitch 2016). Besides, Dubois et al. (2013) highlighted *SIERF5*, *AtERF5*, and *AtER6* as central regulators of salt and drought stresses. It is worth mentioning that *AtERF6* stimulates the expression of different osmotic stress-responsive genes such as *STZ*, *MYB51*, and *WRKY33*.

13.3.5 Auxins

Indole-3-acetic acid (IAA) is the most common phytohormone of the auxin family involved in signalling and several aspects of plant growth and responses to environmental conditions (Jin et al. 2021). Auxins are deemed as the first phytohormones to be characterized (Masuda and Kamisaka 2000), being IAA the most abundant and versatile (Zhao 2010), yet the mechanisms governing IAA biosynthesis, transport, and signalling pathways are still to be elucidated (Wang et al. 2015). This is due to the complexity of the process itself. Available data suggest that the amino acid tryptophan (Trp) acts as a precursor or the major IAA precursor (Fig. 13.1). The conversion of tryptophan to IAA has also been reported (Bartel 1997). Coleoptile tips excised tissues with ^{14}C-Trp-seeds (kernels) of maize (*Zea mays* L. cv. Golden Cross Bantam 70) have shown label incorporation, demonstrating the conversion of tryptophan into IAA (Koshiba et al. 1995). Moreover, IAA can release from IAA conjugates through the hydrolysis of IAA-amino acids, IAA-sugar, and IAA-methyl ester (Bartel 1997; Qin et al. 2005).

IAA acts as a plant growth regulator. It induces cell elongation (Rayle and Cleland 1992), differentiation of cell and vascular tissues (Ding and Friml 2010; Casanova-Sáez et al. 2021) and axial elongation (Campanoni and Nick 2005). It acts as a mediator of apical dominance (Booker et al. 2003). The role of IAA extends to influencing gametogenesis (Zhao 2010), embryogenesis (Cheng et al. 2007), seedling growth (Hu et al. 2017), vascular patterning (Berleth et al. 2000), and flower development (Cheng and Zhao 2007).

IAA plays an integral part in plant adaptation to drought, heavy metal, salinity, and fungal stresses by increasing root and shoot growth at the transcriptional level (Yuan et al. 2013; Tiwari et al. 2020). In tobacco, it has been shown that auxin-inducible glutathione S-transferase (GST), PjGSTU1 from *Prosopis juliflora* confers drought tolerance (George et al. 2010; Cicero et al. 2015). In *Arabidopsis*, increased endogenous levels of IAA-inducing drought tolerance were attained by the activation of flavin monooxygenase encoding genes involved in the tryptophan-dependent IAA biosynthesis pathway (Niyogi and Fink 1992). Similar results were obtained by overexpressing *YUCCA7* in *Arabidopsis* (Lee et al. 2012). Induction of the *OsGH3–2* gene encoding an enzyme for IAA activation in rice subjected to water deficit exhibited drought resistance (Ahammed et al. 2013). Furthermore, the *OsPIN* gene family, particularly *OsPIN2* and *OsPIN5b,* was upregulated under drought stress (Lu et al. 2015) and *TLD1/OsGH3.13*—an IAA amino synthetase encoding gene—overexpression stimulated LEA, leading ultimately to drought tolerance (Rao et al. 2014).

13.3.6 Cytokinins (CKs)

Natural forms of CKs occur as N^6 substituted adenine derivatives, with distinct substitutions attached to the N^6 position of the adenine ring (Fig. 13.1). N^6-(Δ^2-isopentenyl)-adenine (iP), trans-zeatin (tZ), cis-zeatin, and dihydrozeatin are the most common forms. The significant derivatives are tZ, iP, and their sugar conjugates (Sakakibara 2021). CKs are biosynthesized in roots. The addition of the prenyl group derived from the prenol phosphate, named dimethylallyl diphosphate, to the N^6-terminus of ADP/ATP constitutes the first step catalyzed by isopentenyl transferase (IPT), a multigene family that is encoded in most plants

(Kakimoto 2001; Sakakibara 2021). Cytochrome P450 enzymes, CYP735A1 and CYP735A2, participate in the hydroxylation of the isoprenoid side chain, which converts the resulting iP-ribotides into tZ-type CKs (Wheeldon and Bennett 2021). CKs then move the xylem upward to other plant parts, functioning as long-distance messengers to regulate plant growth and development (Aloni et al. 2006; Dun et al. 2006). Prominent roles include cell division (Riou-khamlichi et al. 1999), sink/source relations and nutrient uptake (Roitsch and Ehneß 2000), phyllotaxis (Reinhardt 2004), and gametophyte and embryonic development (Wybouw and De Rybel 2019).

CKs regulate protective responses in plants under abiotic stresses from roots to shoots (Wu et al. 2021). The local stress sensed by roots might implicate changes in the levels of CKs in different plant organs, leading to the plant's drought adaptation, thanks to an enhanced apical dominance stimulated by reduced CK levels (O'Brien and Benková 2013). It has been reported that deregulation of CKs (up- or downregulation) leads to drought tolerance. Enhanced endogenous CK levels were registered in transgenic plants expressing an *IPT* gene, resulting in delayed senescence by suppressing drought-induced leaf senescence. Overexpression of CK oxidase/dehydrogenase (CKX; EC. 1.5. 99.12), which catalyzes CK breakdown, improved drought tolerance possibly due to endogenous plant hormone concentration reduction (Prerostova et al. 2018).

A suggested model, under environmental stresses, revealed that *IPT* gene expression decreases, leading to a decrease in CKs accumulation. Consequently, the triggered expression of stress-responsive genes, following the alleviation of the inhibitory effect of CK signalling, leads to an enhanced plant tolerance. Results displaying altered activity of CK metabolic enzymes in mutant and transgenic cells and tissues corroborate it (Nishiyama et al. 2011). CKs are believed to negatively regulate the branching and growth of roots (Tessi et al. 2021). CKs are degraded under drought stress, thereby enhancing primary root growth and branching (Werner et al. 2010). Batool et al. (2019) reported that two wheat (*Triticum aestivum* L.) genotypes, Heshangtou and Longchun 8275, were subjected to a cascade of water deficit treatments ranging from 80 to 45% reduced CK concentration and closed stomata, resulting in less gas exchange. These changes improved antioxidant machinery and osmotic regulation, leading to enhanced WUE. Altogether, these findings pointed out the CK implication in the root-to-shoot signaling process under environmental stress.

13.3.7 Gibberellins (GA)

GAs form a large group of naturally tetracyclic diterpenoid carboxylic acids based on their ent-gibberellin carbon skeletal structure. GAs range from GA1 to GA136 and are present in 128 vascular plant species (Sponsel and Hedden 2010). The biosynthesis of GAs occurs in the plastid from trans-geranylgeranyl diphosphate, via the methylerythritol phosphate pathway (Kasahara et al. 2002), through the plastid-localized sequential action of two terpene cyclases (Fig. 13.1). The following step is the oxidation by cytochrome P_{450} monooxygenases, which occurs in the endoplasmic reticulum, and then by soluble 2-oxoglutarate-dependent dioxygenases (Yamaguchi 2008). The dioxygenases involve the GA 20-oxidase and GA 3-oxidase families of isozymes, whereas the GA 2-oxidases (GA2ox), another class of dioxygenases, lead to the formation of inactive products in order to enable GA turnover. Drought tolerance is promoted by reducing the endogenous GA level in plants (Colebrook et al. 2014; Zhou et al. 2020). *Arabidopsis* gibberellin methyl transferase1 (*AtGAMT1*) gene was shown to encode an enzyme that catalyzes the methylation of active GA—generating GA methyl esters—resulting in drought tolerance improvement. The overexpression of the *SiDREB* gene was shown to suppress GA biosynthesis genes and increase drought tolerance (Nir et al. 2014; Ullah et al. 2018b).

Besides, *GA2ox* genes are considered to be the most receptive genes to abiotic stress (Ben Saad et al. 2020; Li et al. 2021b). A previous study suggested that restrained plant growth due to exposure to abiotic stress can be partially mediated by DELLA (Asp-Glu-Leu-Leu-Ala) protein—a negative regulator of GA signaling—acting downstream of the GA receptor (Yoshida et al. 2014). Upregulation of specific *GA2ox* genes by dehydration-responsive element binding proteins/C-repeat binding factor (DREB/CBF) family belonging to APETALA2 (AP2) family TFs regulates the expression of stress-responsive genes (Martin et al. 2021). The most significant role of GAs under abiotic stress appears to be associated with cell elongation, as they stimulate DELLA proteins to regulate gene expressions under water scarcity (Krugman et al. 2011). The genotypes of wheat drought-resistant, Y12-3, and drought susceptible, A24-39, subjected to 7-day drought stress, showed shifts in the expression of gibberellin-related genes.

13.3.8 Brassinosteroids (BRs)

BRs are a group of polyhydroxy steroidal plant hormones. Over 70 BRs have been characterized in plants. The most bioactive BRs are brassinolide, 28-homobrassinolide, and 24-epibrassinolide, and they are ubiquitous in the whole plant (Bajguz and Hayat 2009). The first steps in the biosynthesis of BRs are arguably the conversion of campesterol into campestanol, which is later converted to castasterone (Fig. 13.1). These reactions can occur via early or late C-6 oxidation. Finally, castasterone is transformed into brassinolide, which is the first isolated brassinosteroid. Further investigation into the BRs biosynthesis pathways revealed transformations between teasterone and typhasterol via 3-dehydroteasterone. Available data indicates that early and late C-6 oxidation pathways occur in many plants (Hu et al. 2021). BRs act in stem and root growth (Wei and Li 2016), floral initiation (Clouse 2008), and the development of flowers and fruits (Ali et al. 2021). BRs can mitigate abiotic stresses such as high-temperatures (Chen et al. 2021a), salinity (Vázquez et al. 2019), drought (Farooq et al. 2009; Chen et al. 2021b), flooding (Wani et al. 2016), metals/metalloids (Kour et al. 2021), and organic pollutants (Ahammed et al. 2013) by modulating antioxidant machinery components. BRs bind to BR-Insensitive 1 (BRI1) Leucine-Rich Repeat (LRR)-RLK family members on the plasma membrane in response to environmental stress. A ligand elicits BRI1 to act together with the co-receptor BRI1 Associated Receptor Kinase 1, primordial for early BR signalling events (He et al. 2000; Anwar et al. 2018). This is followed by the initiation of a signalling cascade of phosphorylation governing multiple BR-regulated gene expression through BRI1-EMS-SUPPRESSOR1 (*BES1*) and Brassinazole Resistant1 (*BZR1*) TFs (Fàbregas et al. 2018). *WRKY* TFs were implicated in plant growth and response to water deficit stress. *AtDWF4* gene confers better growth, yield, and tolerance against drought in *Brassica napus* (Sahni et al. 2016). Farooq et al. (2009) corroborate the role of BRs in rice subjected to 50% field capacity (FC) water limitation after exogenous application of BRs, 28-homobrassinolide and 24-epibrassinolide, which the cv. Basmati showed drought tolerance by modulating leaf water economy and growth promotion.

13.3.9 Strigolactones (SLs)

SLs are a group of terpenoid lactones that are derived from carotenoids (Fig. 13.1). They play a crucial role in developing the overall root architecture (Xu et al. 2021). SLs play a crucial role in the germination of seeds and plant-microorganism interactions (Mitra et al. 2021). Treatment of strigolactone-response mutant (MAX2) *Arabidopsis thaliana* seedlings with GR24 (a synthetic and biologically active strigolactone) did not repress the lateral root formation, suggesting that the negative effect of strigolactones on lateral root formation is MAX2-dependent (Kapulnik et al. 2011). While SLs are synthesized and exuded essentially in roots, they can be produced in other plant parts (Bradley and Lumba 2021). Moreover, cytochrome P450 and MAX (more axillary growth) genes were displayed to operate SL biosynthesis (Yoneyama and Brewer 2021). A new class of Fe-containing protein, D27, was also identified as an SL biosynthetic element (Lin et al. 2009).

SLs are generally influenced by environmental stimuli and act on shoot and root architecture depending on nutritional conditions (Raza et al. 2021). SLs act in drought acclimatization in plant shoots, while their biosynthesis is suppressed in roots. Since SLs are transported acropetally, their downregulation can indicate affected shoots (Visentin et al. 2016). SLs act as signalling molecules in nodulation during the legume-rhizobium interactions (Soto et al. 2010; Foo and Davies 2011). In barley, the *HvD14* gene has been shown to encode α/β hydrolase implicated in SL signalling and is an orthologue to *D14* described in rice. All these results highlight the potential of SLs to mitigate drought stress (Marzec et al. 2020).

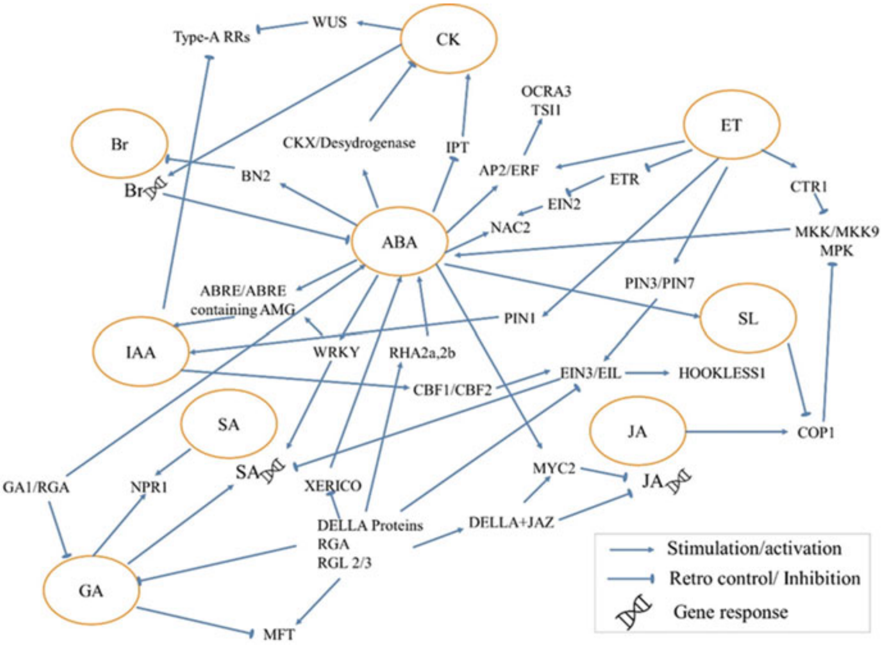

Fig. 13.2 Schematic presentation of potential crosstalk between phytohormone signalling in cereals under drought stress conditions. ABA is the key operating phytohormone against drought stress due to its ability to adapt to stress signals and address downstream stress responses. Stress adaptation regulation is directly controlled by synergistic/antagonistic crosstalk between ABA and other phytohormones. *CDK* cyclin-dependent kinase, *CKX* cytokinin oxidase/dehydrogenase, *COP1* E3 ubiquitin ligase constitutive photomorphogenic 1, *CTR1* constitutive triple response, *EIL* ethylene insensitive-like protein, *EIN2* membrane protein ethylene insensitive 2, *ERF* ethylene response factors, *ETR* ethylene receptor, *HOOKLESS* ethylene response gene, *MAPKKK/MPK* mitogen-activated protein kinase, *MFT* mother of FT and TFL1, *MYC2* helix-loop-helix (bHLH) transcription factor, *NPR1* non-expressor of pathogenesis-related gene 1, *PIN1/3/7* efflux proteins PIN FORMED 1/3/7, *RHA2A-E3* ubiquitin-protein ligase, *Type A RR* response regulator, *WUS* homeodomain transcription factor Wuschel

13.4 Hormone Signalling Crosstalk in Cereal Under Drought Stress Conditions

ABA, JA, ET, and SA are primal actors in drought stress mitigation, where ABA plays a leading role in controlling osmotic stress (Lata and Prasad 2011) (Fig. 13.2). GA, BRs, IAA, SLs, and CKs also act with stress-related gene factors and other phytohormones to sustain plant growth under drought stress. Increasing ABA level under water deficiency was closely linked with ABA-gene activation (Du et al. 2010), thereby inducing drought resistance through stomatal closure and osmolyte accumulation (Tiwari et al. 2017). SA and JA were also shown to be critical factors in water stress signalling based on their increase during this stress and their overall beneficial controlling role in drought resistance mechanisms such as stomatal closing (Savchenko et al. 2014; Tiwari et al. 2016). JA or MeJA (methyl-JA) is converted into an active form JA-Ile ((+)-7-iso-Jasmonoyl-L-isoleucine) after their exogenous supplementation to plants. JA-Ile gets bounded by the SCF-COI complex receptor, which has the COI1 (coronatine insensitive1) F-box protein (Fonseca et al. 2009). This action induces the degradation of JAZ (Jasmonate ZIM-domain) repressors, leading to the JA response gene activation by MYC2 (helix-loop-helix transcription factor 2) (Thines et al. 2007). In the absence of JA, JAZ blocks MYC2, which is then incapable of activating JA-inducible gene transcription. During the stress response, GA in interaction with SA and its exogenous supplementation induced the *NPR1* expression and SA-related genes implicated in SA effect.

ABA also regulates the BR signalling pathway through *BIN2* or its upstream components via the protein phosphatase 2C (*PP2C*) gene family (Zhang et al. 2009). Under drought stress, ABA also restrains BR-induced responses in plants (Divi et al. 2010). CKs regulate the drought stress responses that reduce the biosynthesis and transport of CKs (Tran et al. 2010). Both auxins and BRs, with the presence of MeJA, activate ACO (1-aminocyclopropane-1-carboxylic acid oxidase) enzymes that increase ethylene production (Arraes et al. 2015).

13.5 Factors Modifying the Phytohormonal Activity in Conferring Drought Tolerance in Cereal

Plants are deeply influenced by environmental factors such as light, temperature, infection by microorganisms (beneficial or pathogenic), low nutrients, precipitation, and contamination with metals. These external stimuli affect phytohormone levels in all plant tissues. Therefore, phytohormones are considered a challenge that limits an accurate understanding of plant physiology changes and reaches the mechanistic insight of the implication of phytohormones in regulating drought stress tolerance. Nevertheless, applying natural and chemical substances, minerals, organic amendments, and beneficial microorganisms is the most effective approach for inducing the resistance of plants to drought stress.

13.5.1 Substances, Minerals, and Organic Amendments

Applying priming agents such as injuries or exogenous substances could prepare the plant to respond faster and more effectively against future stresses. A recent study reported that primed wheat plants with polyethylene glycol (PEG) solution maintained higher water potential, increased net photosynthetic rate and proline and GB levels for better dehydration resistance, and activated ABA receptor *PYL4* gene that regulates stomatal closure (Wang et al. 2021a) (Table 13.1). The application of other polymers, such as chitooligosaccharides, chitosan (Ch) and Ch nanoparticles, stimulated plant growth and alleviated water stress in cereals (Zou et al. 2015; Behboudi et al. 2018; Hafez et al. 2020; El Amerany et al. 2020; Almeida

Table 13.1 Effect of external stimuli on phytohormones and drought tolerance in cereals

Factors	Plant species	Effects	Reference
PEG priming	Wheat	Induction of phytohormone signalling (ABA), stress *defense*, and cell elongation gene expression	Wang et al. (2021a)
Zinc foliar application	Maize	Increased IAA and GA level Higher RWC and antioxidant enzyme activity (CAT and SOD)	Moghadam et al. (2013)
Formulated Fertilizer Synergist: 18% N + 2.7% P + 8.3% K + urease and nitration inhibitors + bioactive substances	Rice	Induction of ABA accumulation in roots and leaves Net photosynthetic rate improvement	Wang et al. (2007)
Humic acid	Rice	Increase of endogenous ABA level in leaves and roots	García et al. (2014)
Arbuscular mycorrhizal fungi *Rhizophagus irregularis*	Maize	Decreased ABA content in roots	Li et al. (2016)
Rhizophagus irregularis, strain EEZ 58 + salicylic acid	Maize	Increased IAA, SA, JA, and JA-ile levels in roots	Quiroga et al. (2018)
Glomus microaggregatum, *Rhizophagus irregularis*, *Funneliformis mosseae*, *F. geosporum*, and *Claroideoglomus claroideum*	Rice	Increased IAA and ABA levels in leaves	Chareesri et al. (2020)
PGPR *Azospirillum lipoferum* strain USA 59b	Maize	Enhanced ABA and GA level increased plant length, leaf area, shoot and root dry biomasses	Cohen et al. (2009)
Azospirillum sp.	Wheat	IAA produced by bacteria enhanced plant growth and yield plant water potential and content adjustment	Arzanesh et al. (2011)
Pseudomonas fluorescent (*Ps fluorescent*) strain 153 and 169 and Ps putida strain 4 and 108	Maize	Improved GA, IAA, Cks, and ABA in plant tissue Increased proline content in leaves	Ansary et al. (2012)
Rhizobium leguminosarum, *Mesorhizobium ciceri*, and *Rhizobium phaseoli* (MR-2)	Wheat	IAA produced by bacteria improved plant growth and drought tolerance index	Hussain et al. (2014)
Rhizobacteria (*Bacillus pumilus* (*B. pumilus*); *Ps* sp.; *B. cereus*; *Proteus* sp.; B. *pumilus* + *Ps* sp.; *Proteus* sp. + *Ps* sp.) applied individually or combined with L-tryptophan	Maize	Increased IAA, ABA, and GA levels in leaves Higher osmotic potential, protein, and photosynthetic pigment content	Yasmin et al. (2017)
Azospirillum lipoferum + *Ps putida* + super absorbent polymer	Maize	Increased ABA level and proline Downregulation of the antioxidant enzymes (CAT and GPX)	Moslemi et al. (2011)

et al. 2020). Polymers' effects are due either to their structures containing free amino groups-NH_2 that could interact with ROS or to their ability to decrease the concentration of malondialdehyde (MDA) and electrolyte leakage (EL) and to improve the photosynthetic efficiency, diameter of vascular bundle, RWC, and antioxidant enzymes (i.e., POD, SOD, and CAT) activity (Hidangmayum et al. 2019; El Amerany et al. 2020). However, the effects of these polymers on hormone levels in cereals have not yet been investigated. Zhang et al. (2018) reported that the exogenous supplementation of Ch improved ABA, CKs, and GA levels under drought stress conditions but reduced IAA in white clover (*Trifolium repens* L.).

The application of mineral nutrients (i.e., zinc and ZnO nanoparticles) either to leaves or roots and organic amendments (i.e., formulated fertilizer synergist, biochar, vermicompost, humic acid, and compost) has been commonly applied in agriculture to increase seedling growth and to alleviate drought stresses in cereals (Wang et al. 2007; Moghadam et al. 2013; García et al. 2014; Sun et al. 2020; Ding et al. 2021). Their effects are related to the modulation of phytohormone levels implicated in stress tolerance (Table 13.1). The mineral imbalance in the soil (starvation or accumulation) negatively affected the hormonal interaction between the above-ground and underground parts of plants (Battal 2004). It has been shown that phosphate starvation increased ABA production in roots and inhibited the translocation of CKs from roots to shoots of barley plants, which therefore inhibited roots extension and vacuolar invertase activity and reduced ATP content (Werner et al. 2008; Vysotskaya et al. 2016; Vysotskaya et al. 2020). The excess supply of phosphate increased the ethylene response, which reduced the acquisition of other nutrients (Fe, Zn, Mn, Ca) and the number of meristematic cortical cells and inhibited the growth of the primary root (Shukla et al. 2017).

Organic amendments are considered essential components of soil organic carbon and are well known as biostimulants that may achieve phytohormone-like effects to stimulate nutrient absorption (Canellas et al. 2020). For instance, the application of humic acid to rice seedlings activated plasma membrane H^+-ATPase and increased the activity of calcium-dependent protein kinases (CPKs/CDPKs) implicated in phytohormone production and signalling (Ramos et al. 2015; Xu and Huang 2017). Additionally, the application of seaweed extract (SWE) that contains osmoprotectants (i.e., GB) and phytohormones mixtures (IAA, GA, and CKs) decreased the oxidative damage of wheat grown under limited water supply by inducing the biosynthesis of ascorbate and CAT (Kasim et al. 2015). Shemi et al. (2021) reported that the individual application of GB, Zn, or SA increased the growth of maize seedlings under drought conditions due to their ability to stabilize chlorophyll pigments, maintain water equilibrium, decrease ROS and MDA content, and increase gas exchanges, RWC, and antioxidant enzymes (SOD, CAT, POD, glutathione reductase (GR), and ascorbate peroxidase (APX)). Although there is scarce information about SWE functioning to alleviate drought, they could positively affect the expression of genes responsible for host hormonal biosynthesis, like auxin (Ali et al. 2021).

13.5.2 Beneficial Microorganisms

Other strategies plants adopt to deal with (a)biotic stresses, especially drought, are interaction with beneficial soil microbes, including plant growth-promoting fungi (e.g. arbuscular mycorrhizal fungi (AMF)) and rhizobacteria. Significantly, the ‘cry-for-help’ strategy suggests that plants recruit beneficial microorganisms to resist environmental stresses by changing their root exudation chemistry (Rizaludin et al. 2021). These microorganisms have been described as effective biofertilizers for host plant growth-boosting, encompassing all the dynamic processes of growth, metabolism, and defense (Ait-El-Mokhtar et al. 2020; Anli et al. 2020; Ben-Laouane et al. 2021; Boutasknit et al. 2020; El Amerany et al. 2020; Hossain and Sultana 2020).

13.5.2.1 Plant Growth-Promoting Fungi (PGPF)

PGPF are nonpathogenic saprotroph fungi that have shown increasing interest in recent years due to their benefits, especially in promoting crop production and potentiating tolerance against stresses (Hossain and Sultana 2020; Cornejo-Ríos et al. 2021). These fungi could alter the physiology and biochemical processes of the host plants through various strategies, including the conversion of the insoluble phosphate to a soluble form, mineralization of organic substrate, production of enzymes, volatile compounds (i.e., sesquiterpenes and diterpenes), and phytohormones (Hossain and Sultana 2020). Several studies reported that *Trichoderma atroviride* ID20G application to maize seedlings reduced the injurious effects of water stress by stimulating photosystem II efficiency (F_v/F_m), pigment contents, and antioxidant enzyme activity (Guler et al. 2016). While no report related to phytohormone changes in cereals under water deficiency, either *Phoma glomerata* LWL2 or *Penicillium* sp. LWL3 application to cucumber seedlings mitigated water deficit by impairing polyphenol oxidase activity and reducing glutathione and endogenous SA, JA, and ABA levels that could impact GAs and IAA secretion (Waqas et al. 2012).

Arbuscular mycorrhizal fungi (AMF) could form symbiotic interactions with more than 70% of terrestrial plants (Cosme et al. 2018). Many reports showed that AMF-inoculated plants increased height, number and length of lateral roots, leaf area, number of flowers and fruits, and dry matter production (Elhindi et al. 2017; Boutasknit et al. 2021; Vosnjak et al. 2021). For instance, the plant weight of rice was ten times higher in *Glomus intraradices* inoculated plants than in non-inoculated plants (Ruíz-Sánchez et al. 2011). Moreover, the mutualistic relationship between plants and AMF is regulated by phytohormones. Some SLs are involved even before physical contact between the fungi and the host plants, whereas others are accumulated only at a late stage of mycorrhization (i.e., CKs) (Mitra et al. 2021). In addition, some phytohormones are accumulated to regulate root system architecture and fungal development (i.e., IAA, ABA, and JA) (Akiyama and Hayashi 2006; Hause et al. 2007). In rice, the overexpression of *OsNAC14*, a TF that is implicated in drought stress tolerance, induced SL biosynthesis (Shim et al. 2018). Nevertheless, the effect of CKs on the establishment of mycorrhization and water stress tolerance is still not well understood; specific authors pointed out that the accumulation of these hormones was positively correlated with the photosynthesis rate increase and fungal growth (Werner et al. 2001). Inoculation of *Catalpa bungei* with *Rhizophagus intraradices* reduced the content of zeatin in well-watered plants and those exposed to water deficiency (Chen et al. 2020). These findings showed that mycorrhization rate and the level of other hormones, IAA and ABA, were not adversely affected. Also, the level of phytohormones might vary between plant cultivars. For instance, in maize, while cv. B73 inoculated with *R. irregularis* reduced ABA levels, however, PR34B39 cv increased them (Table 13.1). Furthermore, a metabolomic study revealed that the inoculation of durum and bread wheat roots with *Funneliformis mosseae* under drought stress increased the levels of brassinosteroids (6 alpha-hydroxy-castasterone and brassinolide-23-O-glucoside), hydrolyzable abscisic acid (D-glucopyranosyl abscisate), a hormone similar to IAA (indole-3-acetyl-methionine), gibberellins (gibberellin A29-catabolite and gibberellin A34-catabolite), and jasmonate derivative (tuberonic acid glucoside) in roots (Bernardo et al. 2019).

13.5.2.2 Plant Growth-Promoting Rhizobacteria (PGPR)

The PGPR are beneficial bacteria that positively influence the growth and yield of different crops (Oleńska et al. 2020). They could fix and convert atmospheric N to ammonia, transform soil macromolecules into easily available compounds for plants, solubilize soil phosphate, release organic acids, and produce exopolysaccharides (EPS) and phytohormones (i.e., CKs, IAA, GA_3, and zeatin) to alleviate drought stresses (Martínez-Viveros et al. 2010; Vardharajula et al. 2011; Zaheer et al. 2019). EPS are organic polymers made by bacteria to contact the host plants (Naseem et al. 2018). Despite the vital role of EPS in drought stress tolerance, their role in modulating phytohormone levels is unknown. A previous study showed that applying one or multiple rhizobacterial strains, individually or combined with either L-tryptophan or super absorbent polymer, significantly increased plant performance (Table 13.1). This positive effect is due to increased osmotic potential, proline and sugar content, antioxidant enzyme activity, ABA, GAs, CKs, and IAA levels (Table 13.1).

13.6 Metabolic Engineering of Phytohormones: New Strategies in Cereal to Mitigate Drought Stress

Using the most tolerant plant species to water stress and increasing cereal resistance through making crosses between inbred lines or applying a transgenic approach are considered the best-applied strategies for improving cereal productivity and minimizing land consumption of freshwater resources (Parmar et al. 2017). These advanced lines are characterized by deregulating genes of interest and stimulating regulatory factors (proteins) involved in the biosynthesis of metabolites, especially phytohormones, to ensure drought tolerance.

13.6.1 Breeding

Developing new drought-tolerant cereal lines using natural breeding becomes an important strategy. This technique provides changes in plant traits and creates plants with desirable characteristics based on crossing lines selected based on their high WUE or lines with contrasting phytohormone levels (Bruce et al. 2002). Despite the applicability of this approach to a broad type of plant species, however, it did not meet the general need yet, owing to the long time it takes to minimize linkage drag through phenotypic screening. Successful findings were reported in maize. For example, Pekić et al. (1995) reported that crossing maize lines "Polj17" (high ABA level) x F-2 (low ABA level) increased yield and ABA level in both leaves and kernels and reduced transpiration in the offspring compared to the parents. Moreover, the maize inbred line "RIL70", from crossing Ph4CV × F9721, was more tolerant to stress than parental lines due to its ability to detoxify stress signals through increasing photosynthetic rate, cell wall biosynthesis, and the early expression of aquaporin-related genes. Min et al. (2016) reported that ABA level and *bZIP* gene expression involved in ABA synthesis and *ABRE* TFs were induced in the "RIL93" line (drought-sensitive) compared to the "RIL70" line.

13.6.2 Genetic Engineering

Genetic engineering is of the utmost importance for cereal growers since it offers a fast and exact way to attain the same objective as breeding crops for certain desirable traits in one generation rather than multiple. To achieve this goal, new cultivars are created by employing wild genes involved in drought tolerance, selecting marker-assisted breeding, and isolating trait locus genes (Khan et al. 2019). Plants could alleviate the deleterious effects of drought stress by stimulating the expression of TFs, i.e., *NAC*, *MYB*, *bZIP*, *HDG*, and *WRKY*, that activate phytohormone biosynthesis genes at the transcriptional level and deregulate the expression of stress-related genes (He et al. 2016; Shim et al. 2018). In rice, Shim et al. (2018) reported that overexpression of *OsNAC14* induced SL biosynthesis and diminished DNA damage and the expression of drought-responsive marker genes (*OsDIP1*, Dehydration Stress-Inducible Protein 1, and *OsRbcS*, Small Subunit of Rubisco). Overexpression of *OsMYB6* in rice could play a pivotal role in minimizing drought stress injuries because it elevated the expression of the NAC gene (*SNAC1*) (Tang et al. 2019). Overexpression of *OsHBP1b* in rice plants boosted plant growth and development and increased callose and antioxidant enzyme levels (Das et al. 2019).

Transgenic wheat plants over-expressing *AtHDG11* and *TaWRKY2* showed better growth than wild type plants. These transgenic plants are characterized by lower stomatal density, higher WUE, and accumulation of osmotically active molecules (i.e., proline, chlorophyll, and sugars, CAT, and SOD) to detoxify ROS molecules (Li et al. 2016; Gao et al. 2018). Exogenous application of phytohormones, such as BRs, induced *OsDof12*-type TFs in rice plants; however, the overexpression of *OsDof12* in plants negatively regulated BRs signalling genes and affected plant cell architecture (Wu et al. 2015). Overexpression of *JERF1*, involved in ET biosynthesis, in rice exhibited better shoot and root development and a higher level of ABA (Table 13.2).

13.7 Conclusion and Future Perspectives

Drought stress is a constant factor that alters cereals' growth, physiology, and metabolism. Substantial progress has been achieved recently to understand the mechanisms and the role of signalling molecules, such as phytohormones, on plant growth and yield and plant tolerance to environmental stress. As phytohormones upregulate various plant functioning processes, they can control the same traits to manage the adaptation of plants to stressful conditions. Under drought stress, the growth and development of plants are controlled by phytohormones including CKs, IAA, ET, GAs, ABA, JAs, BRs, SA, and SL through signalling cross-talk pathways orchestrated by ABA. These compounds are implicated in the drought adaptation process through stimulating stomatal closure, increasing WUE, metabolite adjustment, and expression of TFs and stress-responsive genes. The phytohormones' cross-talk under water deficiency is carried out at different levels such as hormone activation, transcriptional activation, gene expression, and developmental variations. Despite the significant role of phytohormones in alleviating drought stress, their production and signalling pathways may be hindered owing to the vast difference in plant physiological characteristics and the duration and severity of stress. Therefore, many methods and technologies have been used to retrieve cereals from the negative impact of drought and deregulate the phytohormone concentration involved in tolerance to improve the yield. Selection of drought-tolerant species, exogenous application of minerals and organic amendments, inoculation with beneficial microorganisms (AMF, PGPF, and PGPR), and use of natural breeding/genetic engineering are factors and techniques that could help to boost cereals under future environmental stresses. With the development of omics-based research in recent decades, many gaps still need to be investigated, especially in the molecular mechanisms related to the cross-talk among phytohormones at cellular and transcriptional levels and their transport systems, receptors, mediators, and targets in plants. These aspects are highly complicated, particularly under drought stress. It is worth mentioning that genome-wide studies targeting phytohormone signalling responses under adverse environmental situations are needed and will significantly contribute to a better understanding of hormone interaction with the crosstalk network and developing ultimately effective strategies for improving cereal stress tolerance.

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Table 13.2 Example of phytohormones metabolic engineering for drought stress tolerance in cereals

Hormone	Gene	Gene function	Expression	Plant species	Effects	Reference
ET	*JERF1*	ET response factor proteins	Upregulation	Rice	Reduction in water loss Increase in seedlings fresh weight, root length, proline level, biosynthesis of ABA and its enzyme genes (*OsABA2* and Os03g0810800)	Zhang et al. (2010)
	ACC synthase	ET biosynthesis	Downregulation	Maize	Higher kernel number and grain yield	Habben et al. (2014)
ABA	*LOS5*	ABA biosynthesis	Upregulation	Maize	Reduction in water loss and MDA and H_2O_2 Increase in stomatal closure, root system, antioxidative enzymes activity, ABA level, and the expression of *NCED1* gene	Lu et al. (2013)
	AtNCED6	ABA biosynthesis	Upregulation	Barley	Downregulation of endogenous *HvNCED* better assimilation of water	Seiler et al. (2014)
	OsWRKY5	Inactivate ABA biosynthesis	Downregulation	Rice	Downregulation of endogenous *OsWRKY5* improve drought tolerance in rice	Lim et al. (2021)
Auxin	*TLD1*	IAA biosynthesis	Upregulation	Rice	Dwarf-like phenotype Higher tiller number and IAA-amino acid conjugate	Zhang et al. (2009)
	OsPIN3t	Auxin efflux carrier	Upregulation	Rice	Increase root development and drought tolerance	Zhang et al. (2012)
	OsIAA6	Regulation of auxin biosynthesis	Upregulation	Rice	Increase plant growth, F_v/F_m, and tiller number Reduction of *DIP1* (dehydration marker) transcript	Jung et al. (2015)
CK	*IPT*	CK biosynthesis	Upregulation	Rice	Up regulation of ABA, CK-O-glucosyltransferase, and BR-insensitive1-like precursor genes Down regulation of JAZ1, PP2C7, auxin-induced protein 5NG4, and ethylene-responsive TF genes	Peleg et al. (2011)
	AtCKX1	Vacuole-targeted CK dehydrogenase	Downregulation	Barley	Increase the number of lateral roots and yield and maintain higher level of water content	Pospíšilová et al. (2016)

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