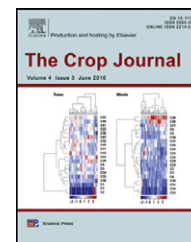
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Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants



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ABSTRACT

Abiotic stresses including drought, salinity, heat, cold, flooding, and ultraviolet radiation causes crop losses worldwide. In recent times, preventing these crop losses and producing more food and feed to meet the demands of ever-increasing human populations have gained unprecedented importance. However, the proportion of agricultural lands facing multiple abiotic stresses is expected only to rise under a changing global climate fueled by anthropogenic activities. Identifying the mechanisms developed and deployed by plants to counteract abiotic stresses and maintain their growth and survival under harsh conditions thus holds great significance. Recent investigations have shown that phytohormones, including the classical auxins, cytokinins, ethylene, and gibberellins, and newer members including brassinosteroids, jasmonates, and strigolactones may prove to be important metabolic engineering targets for producing abiotic stress-tolerant crop plants. In this review, we summarize and critically assess the roles that phytohormones play in plant growth and development and abiotic stress tolerance, besides their engineering for conferring abiotic stress tolerance in transgenic crops. We also describe recent successes in identifying the roles of phytohormones under stressful conditions. We conclude by describing the recent progress and future prospects including limitations and challenges of phytohormone engineering for inducing abiotic stress tolerance in crop plants.

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1. Introduction

The human population is rapidly increasing and needs a substantial increase in agricultural productivity worldwide. However, various biotic and abiotic stresses are major factors limiting crop productivity [1]. To feed the world population, productivity must be increased by 70% for an additional 2.3 billion people by 2050 [2]. The mechanisms underlying environmental stress response and tolerance in plants are different and more complex than animals [3]. Identifying the principles by which plants respond to various environmental stresses is one of the critical aspects for plant biotechnologists. Amongst various abiotic stresses, drought, salinity, and extreme temperatures are most widespread and significant [4]. Because of the complexity of stress tolerance traits, conventional breeding techniques have met with limited success. They demand effective advances to feed the growing worldwide food demand. In this direction, novel and potent approaches should be devised. Engineering of phytohormones could be a method of choice to produce climate-resilient crops with high yields.

Phytohormones are molecules produced in very low concentrations but able to regulate a variety of cellular processes in plants. They work as chemical messengers to communicate cellular activities in higher plants [5]. Phytohormones play key roles and coordinate various signal transduction pathways during abiotic-stress response. They regulate external as well as internal stimuli [6]. Some phytohormones, such as ABA, have been identified as stress hormones. ABA plays critical roles in plant development: maintenance of seed dormancy, inhibition of germination, growth regulation, stomatal closure, fruit abscission, besides mediating abiotic and biotic stress responses [7]. Phytohormone engineering could be a perfect platform for biotechnologists to

improve crops nutritionally and economically. In this review, we present an overview of the phytohormones and their roles in plant growth, development, and abiotic stress response, in addition to their metabolic engineering to confer abiotic stress tolerance in crop plants to increase food quantity and quality. We discuss recent successes and future prospects.

2. Abiotic stresses: Challenging the changing world

Investigating how abiotic stresses affect plant growth and development at the physiological, biochemical, and molecular levels is critical to increasing the productivity of crops, because stresses cause widespread crop losses throughout the world [6]. Environmental factors imposing stress on plants, including drought, salinity, heat, chilling, freezing, ozone, pathogens, and UV radiation are the major environmental cues that limit crop productivity. The period and development of stress, stages of the plant, and biotic and abiotic factors may influence the stress response [8]. Some crops may be affected at an early stage, but recover and finally survive. Susceptibility or resistance to stresses may differ markedly among species or genotypes of crops. Among these stress conditions, drought is perhaps the most severe stress, responsible for decreased agricultural production worldwide. It affects plants in many ways: plant growth, membrane integrity, pigment content, osmotic adjustments, water relations, and photosynthetic activity [9,10]. As rightly pointed out by Postel [11], water will be the oil of the 21st century. Many rivers around the globe are drying daily; most have no water to discharge to the sea [11]. After drought, salinity is the second major stress reducing crop productivity. Various plant hormones have shown positive plant-protective functions

against abiotic stresses and attempts have been made to assign specific hormone(s) for specific stresses as well as combinations of stresses, as some hormones have shown multiple stress-resistance functions.

3. Importance of studying plant stresses in combination

Previously, to study abiotic stress conditions, generally specific stress conditions were investigated, including drought, salinity, or heat, and the diverse molecular aspects of plant acclimation were analyzed. However, conditions differ in the natural environments. In nature, crops face different stresses or combinations of stresses found in the environment. The majority of molecular studies are conducted under controlled conditions in the laboratory or greenhouse and do not reflect the actual conditions that occur in the field. In the laboratory or greenhouse, conditions are controlled so that one stress is imposed, but in natural conditions there are many environmental stresses that are applied in combination. Therefore, the experiments conducted for evaluating effects of a combination of stress factors rather than an individual stress may prove advantageous. Drought and heat stress in combination caused losses of \$200 billion in the USA (readers are encouraged to refer to the excellent review of Suzuki et al. [12]).

4. Phytohormones: Key mediators of plant responses to abiotic stresses

Plants must regulate their growth and development to respond to various internal and external stimuli [13]. Phytohormones, a diverse group of signaling molecules found in small quantities in cells, mediate these responses. Their pivotal roles in promoting plant acclimatization to ever-changing environments by mediating growth, development, source/sink transitions, and nutrient allocation have been well established [14]. Although plant response to abiotic stresses depends on various factors, phytohormones are considered the most important endogenous substances for modulating physiological and molecular responses, a critical requirement for plant survival as sessile organisms [14]. Phytohormones act either at their site of synthesis or elsewhere in plants following their transport [15]. Phytohormones are of key importance in plant development and plastic growth. They include auxin (IAA), cytokinins (CKs), abscisic acid (ABA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), brassinosteroids (BRs), and jasmonates (JAs). The strigolactone (SL) are relatively new phytohormones. Fig. 1 shows the chemical structures of major phytohormones.

4.1. Abscisic acid (ABA), the abiotic stress hormone

Abscisic acid (ABA) owes its name to its role in abscission of plant leaves and is perhaps the most studied phytohormone for its response and distinct role in plant adaptation to abiotic stresses, and is accordingly termed a “stress hormone.” It is an isoprenoid plant hormone produced in the plastidal 2-C methyl-D-erythritol-4-phosphate pathway. ABA

plays an influential during several plant physiological processes and developmental stages including seed dormancy and development, stomatal opening, embryo morphogenesis, and synthesis of storage proteins and lipids [16].

ABA is considered an essential messenger in the adaptive response of plants to abiotic stress and its role in stress tolerance has received much attention. In response to environmental stresses, endogenous ABA levels increase rapidly, activating specific signaling pathways and modifying gene expression levels [17]. Nemhauser et al. [18] have reported that ABA transcriptionally regulates up to 10% of protein-encoding genes. ABA also acts as an internal signal enabling plants to survive under adverse environmental conditions [19].

Under water-deficit conditions, ABA plays a vital role in providing plants the ability to signal to their shoots that they are experiencing stressful conditions around the roots, eventually resulting in water-saving antitranspirant activity, notably stomatal closure and reduced leaf expansion [20]. ABA is also involved in robust root growth and other architectural modifications under drought stress [21] and nitrogen deficiency [22]. ABA regulates the expression of numerous stress-responsive genes and in the synthesis of LEA proteins, dehydrins, and other protective proteins [23,24]. ABA upregulates the processes involved in cell turgor maintenance and synthesis of osmoprotectants and antioxidant enzymes conferring desiccation tolerance [25]. Zhang et al. [26] reported a proportional increase in ABA concentration upon exposure of plants to salinity.

4.2. Auxins (IAA)

Although auxin has been studied for over 100 years, its biosynthesis, transport, and signaling pathways are still not clear [27]. However, some interconnecting pathways have been proposed so far for biosynthesis of auxin in plants, including four tryptophan (Trp)-dependent and one Trp-independent pathway [28]. IAA (indole-3-acetic acid) is one of the most multi-functional phytohormones and is vital not only for plant growth and development but also for governing and/or coordinating plant growth under stress conditions [29]. The presence of an auxin biosynthesis, signaling, and transport apparatus in single-celled green algae is clear evidence of the evolutionary role played by auxin during the adaptation of plants to diverse land environments [30]. Though there has been a recent upsurge in our understanding of auxin regulation of plant growth and development, its role as a regulator of stress response is still little understood [29].

Interestingly, there is growing evidence that IAA plays an integral part in plant adaptation to salinity stress [14,31]. It increases root and shoot growth of plants growing under salinity or heavy metal stresses [32,33]. Salinity reduced IAA levels in maize plants, but salicylic acid application effectively increased them [34], indicating that hormonal balance and crosstalk are critical to signal perception, transduction, and mediation of stress response [14]. Auxin stimulates the transcription of a large number of genes called primary auxin response genes, and these genes have been identified and characterized in several plant species including rice, *Arabidopsis*, and soybean [35]. Auxin is regarded as an influential constituent of defense responses via regulation of numerous genes and mediation of crosstalk

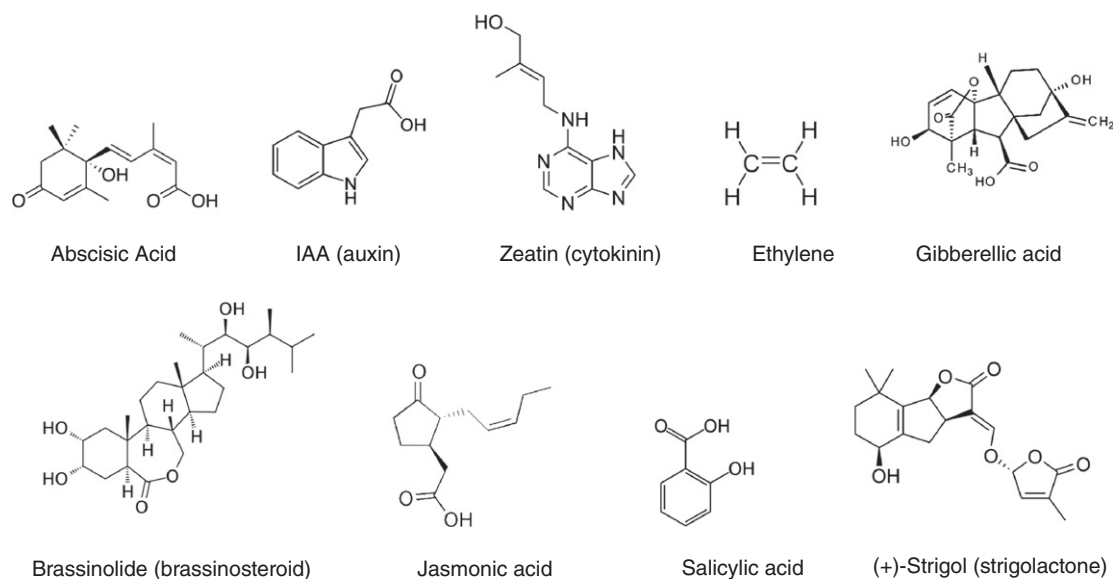


Fig. 1 – Major classes of phytohormones involved in abiotic stress response and tolerance in plants.

between abiotic and biotic stress responses [36]. However, identification of novel genes involved in stress responses may prove to be a vital target for engineering abiotic stress tolerance in principal crops.

4.3. Cytokinins (CKs)

CKs play influential roles in many plant growth and developmental processes and are considered as master regulators during plant growth and development [37,38]. Alteration of endogenous levels of CKs in response to stress indicates their involvement in abiotic stress [17], including drought [37] and salinity [38]. Mutants and transgenic cells/tissues with altered activity of cytokinin metabolic enzymes or perception machinery points toward their crucial involvement in several crop traits including productivity and increased stress tolerance [39].

Although plant responses to CKs have been evaluated most often via their external application, stressful conditions are also known to enhance their endogenous levels via uptake and enhanced biosynthesis [40]. In contrast to the ABA inhibition of seed germination, they also release seeds from dormancy [36]. CKs are often considered ABA antagonists [41]. In water-stressed plants, decreased CK content and accumulation of ABA lead to an increased ABA/CK ratio. The reduced CK levels enhance apical dominance, which, together with the ABA regulation of stomatal aperture, aids in adaptation to drought stress [17].

4.4. Ethylene (ET)

ET, a gaseous phytohormone, is involved in several phases of plant growth and development, notably fruit ripening, flower senescence, and leaf and petal abscission, besides being an essential regulator of stress responses [42,43]. It is biosynthesized from methionine via S-adenosyl-L-methionine (*AdoMet*) and the cyclic non-protein amino acid ACC. ACC synthase convert

AdoMet to ACC, while ACC oxidase catalyzes the conversion of ACC to ethylene.

Abiotic stresses including low temperature and salinity alter endogenous ET levels in plants. Enhanced tolerance was accordingly achieved with higher ET concentrations [44]. ET also plays a major role in the defense response of plants to heat stress [45]. Environmental stress induces ET accumulation which increases plant survival chances under these adverse conditions [42]. ET has been proposed to function via modulation of gene expression considered as the effectors of ethylene signal [46].

ET in combination with other phytohormones such as JA and SA often acts cooperatively. These are considered the main players involved in regulating plant defense against pests and pathogens [6]. The biosynthesis, transport, and accumulation of these hormones trigger a cascade of signaling pathways involved in plant defense [47]. As concluded by Yin et al. [48], ET and ABA seem to act synergistically or antagonistically to control plant growth and development.

4.5. Gibberellins (GAs)

The gibberellins (GAs) are a large group of tetracyclic diterpene carboxylic acids, but only a few of them function as growth hormones in higher plants, predominant forms being GA₁ and GA₄ [49]. The GAs show positive effects on seed germination, leaf expansion, stem elongation, flower and trichome initiation, and flower and fruit development [50]. They are essential for plants throughout their life cycle for growth-stimulatory functions. They also promote developmental phase transitions [51]. Interestingly, there is increasing evidence for their vital roles in abiotic stress response and adaptation [51]. Recently, experiments have been performed to investigate the role of GAs in osmotic stress response in *Arabidopsis thaliana* seedlings [52,53]. GAs are known to interact with all other phytohormones in numerous developmental and stimulus-response processes [54]. The interactions between GA

and ET include both negative and positive mutual regulation depending on the tissue and signaling context [54].

4.6. Brassinosteroids (BRs)

Brassinosteroids (BRs) comprise a relatively new group of polyhydroxy steroidal plant hormones with strong growth and development-promoting potential. They were first isolated and characterized in pollen of the rape plant (*Brassica napus*). More than 70 BRs have been isolated from plants. However, brassinolide, 28-homobrassinolide, and 24-epibrassinolide constitute the three most bioactive BRs and are widely used in physiological and experimental studies [55]. They are present in almost every part of plants including pollen, flower buds, fruits, seeds, vascular cambium, leaves, shoots, and roots [56]. They play a critical role in numerous developmental processes such as stem and root growth, floral initiation, and development of flowers and fruits [56].

However, recent findings suggest stress-impact mitigating roles of BRs and associated compounds in various plants subjected to various abiotic stresses. These abiotic stresses are high temperature [57], chilling [58], soil salinity [59], light [60], drought [61], flooding [62], metals/metalloids [63], and organic pollutants [64]. Recent research has shown tremendous potential of BRs and associated compounds in the modulation of components of antioxidant defense system in-response-to and to counteract the abiotic stress-induced oxidative burst, reviewed by Vardhini and Anjum [65]. However, there is tremendous scope for further research focused on the sites, pathways, and enzymology of their biosynthesis, source–sink relationships, developmental and stress physiology, their interactions with microorganisms, fungi, and animals, and the realization of their powerful applications [14].

4.7. Jasmonates (JAs)

The cyclopentanone phytohormones derived from the metabolism of membrane fatty acids including primarily methyl jasmonate (MeJA) and its free acid jasmonic acid (JA) are collectively called jasmonates (JAs) and are widespread in the plant kingdom. These multifunctional compounds are involved in crucial processes associated with plant development and survival including reproductive processes, flowering, fruiting, senescence, secondary metabolism, and direct and indirect defense responses [66,67]. JA is the most abundant, best known, and best characterized of the JAs. In addition to developmental functions of plants, JA activates plant defense responses to pathogenic attack as well as environmental stresses including drought, salinity, and low temperature [68,69]. JAs are vital signaling molecules induced by various environmental stresses including salinity [68], drought [69,70], and UV irradiation [71]. They have great potential to mitigate an array of threatening environmental stresses [72]. The exogenous application of MeJA effectively reduced salinity stress symptoms in soybean seedlings [73]. Remarkably, endogenous levels of JA increased in rice roots under salinity stress and reported to counteract the deleterious effects of salinity stress [74]. JAs applications alleviate heavy metal stress in plants by activating the antioxidant machinery [75]. MeJA confers tolerance in *A.*

thaliana plants against Cu and Cd stress via accumulation of phytochelatins [76].

4.8. Salicylic acid (SA)

Salicylic acid (SA) is a naturally occurring phenolic compound involved in the regulation of pathogenesis-associated protein expression [77]. In addition to defense responses, it plays a vital role in the regulation of plant growth, ripening and development, as well as responses to abiotic stresses [78,79]. The synthesis of SA occurs via two pathways: the isochorismate (IC) and the phenylalanine ammonia-lyase (PAL) pathway. Of these, the major pathway is the IC pathway in *Nicotiana benthamiana* [80] and tomato [81].

An interesting and noteworthy general belief is that low concentrations of SA enhance the antioxidant capacity of plants, but high concentrations of SA cause cell death or susceptibility to abiotic stresses [82]. Most genes that respond positively to acute SA treatment are associated with stress and signaling pathways that eventually led to cell death. SA consists of genes encoding chaperones, heat shock proteins, antioxidants, and genes involved in the biosynthesis of secondary metabolites, such as sinapyl alcohol dehydrogenase, cinnamyl alcohol dehydrogenase, and cytochrome P450 [82].

SA is involved in plant response to abiotic stresses such as drought [83], salinity [34,84], chilling [85], and heat [86]. SA along with ABA is involved in the regulation of drought response [77]. Drought stress induced a five-fold increase in the endogenous levels of SA in *Phillyrea angustifolia* [87]. The SA content in barley roots was increased approximately twofold by water deficit [88]. The SA-inducible genes PR1 and PR2 (pathogenesis-related genes) are induced by drought stress [83]. However, the detailed molecular mechanisms of SA's roles in abiotic stress tolerance remain largely unknown and more comprehensive investigations are needed in this direction.

4.9. Strigolactones (SL)

Strigolactones (SLs) constitutes a small class of carotenoid-derived compounds, first characterized more than 45 years ago as seed germination stimulants in root parasitic plants such as *Striga*, *Orobancha*, and *Phelipanche* species [89,90]. Several types of SLs can be synthesized by single plant species, whereas mixtures of different types and quantities of SL molecules are produced in intraspecific varieties [89,91]. Although they are produced and exuded in small amounts primarily in roots, other plant parts can also synthesize them [92]. A comparative study involving wild-type and mutant *Arabidopsis* plants indicates their role in the development of root system architecture [93]. Application of GR24, a synthetic and biologically active SL [94,95], repressed lateral root formation in wild-type seedlings and SL-synthesis mutants (*max3* and *max4*) but not in the strigolactone-response mutant (*max2*), suggesting the MAX2-dependent negative effect of strigolactone on lateral root formation [93,96]. Apparently, SLs are involved in plant responses to environmental stimuli from their early evolution. In higher plants, they participate in both shoot and root architecture in response to nutritional

conditions [97]. SLs also act as signaling molecules for plant interactions with microbes. They stimulate nodulation in the legume–rhizobium interaction process [98,99]. Overall, it can be concluded that SLs constitute an important group of signaling molecules and are key regulators of plants' developmental adaptations to changing environmental conditions. They have the potential to be used in agriculture for various purposes including as inducers of suicidal seed germination of parasitic plants [100].

5. Crosstalk between phytohormones signaling

Environmental stresses require plants to perceive and react to these signals in a highly coordinated and interactive manner. Plants being sessile organisms need to maintain plasticity in growth and ability to adapt to harsh changing environmental conditions, and this adaptation is mediated by elaborate signaling networks. Signal transduction cascades that interact with the baseline pathways transduced by phytohormones get triggered by the perception of abiotic stresses [101]. The fluctuations of stress-responsive hormones help alter cellular dynamics and thus play a central role in coordinately regulating growth responses under stress conditions [102]. The convergence points among hormone signal transduction cascades are considered crosstalk, and together they form a signaling network [101]. In this way, hormones seemingly interact by activating either a common second messenger or a phosphorylation cascade. In the last few decades, insights into the biosynthetic and core signaling components of major phytohormones including ABA, IAA, BRs, GAs, JA, and ET have been revealed [103]. However, owing to the extreme complexity of responses to different stress thresholds, lack of knowledge about tissue-specific stress response, and inadequate understanding of genetic plasticity and its adaptability to environments, the mechanistic basis of abiotic stress tolerance remains largely unclear and confusing [102]. Consequently, all these factors collectively contribute to more confusion than resolution [104]. Still, perturbed phytohormone fluxes and the subsequent signal transduction cascade have been revealed as one of the primary stress responses evolved by plants.

Various plant hormones interact together for signal defense networking to fine-tune the defense against environmental challenges. Among them, SA, JA, and ABA hold particular importance and are regarded as key players in the regulation of signaling pathways. In recent years, deciphering the interactions between phytohormones and their coordinated roles in counteracting abiotic stresses has gained new attention. Experimental findings unequivocally show that the interactions among phytohormones are the rule rather than the exception in integrating diverse input signals and readjusting growth and acquiring stress tolerance in plants [102]. The presence of multiple and frequent redundant signaling intermediates for each hormone hints at their apparent roles in such crosstalk. Understanding the crosstalk between phytohormonal and defense signaling pathways is thus important, as it may reveal new potential targets for the development of host resistance mechanisms and phytohormones [105].

We now discuss stomatal closure as a rapid response to water deficit conditions and phytohormonal crosstalk in its regulation. Stomatal closure is regulated by a complex network of signaling pathways, and as a short-term response is triggered primarily by ABA. ABA controls long-term growth responses via the regulation of gene expression that favors maintenance of root growth, which optimizes water uptake [26]. However, following the rules of drought stress response, ABA apparently interacts with other plant hormones and signaling molecules such as JA and nitric oxide (NO) to stimulate stomatal closure, whereas its regulation of gene expression includes the induction of genes associated with response to ethylene, cytokinin, or auxin [101]. It has been proposed by the authors that stress-induced JA production interacts with ABA-mediated stomatal closure by stimulating the influx of extracellular Ca^{2+} and/or by activating $\text{H}_2\text{O}_2/\text{NO}$ signaling [101]. In contrast, Desikan et al. [106] provided evidence that stomatal closure by ethylene is regulated via its signal transduction pathway, which both stimulates production and requires H_2O_2 synthesis. This crosstalk also involves JA, whose biosynthesis is induced by stress conditions including herbivory [107], whereas many JA-associated signaling genes are regulated by drought stress [108]. JA interacts with ABA-regulated stomatal closure by increasing Ca^{2+} influx, which ultimately stimulates calcium-dependent protein kinase (CDPK) production and the resulting signal cascade [101]. A 10-min treatment with either ABA or MeJA resulted in a reduction of stomatal aperture in turgid and excised leaves of *Arabidopsis* [109]. The authors postulated that both ABA and MeJA interact in guard cells and induce the formation of reactive oxygen species and NO and that both are present at reduced concentrations in MeJA-insensitive plants. In another experiment, Kim et al. [110] found that drought stress induced a 19-fold increase in MeJA levels and a 2-fold increase in ABA levels, which was associated with severe yield loss due mainly to poor seed set. This phenotype was mimicked by concentrations of MeJA in young panicles of rice through the ubiquitous expression of AtJMT transgenically, which also led to a dramatic reduction in grain yield and a substantial increase in ABA, suggesting crosstalk between MeJA and ABA biosynthesis [110]. Similarly, long-term physiological responses to abiotic stress conditions are caused and influenced by altered ABA-mediated gene regulation of transcription factors (TFs) that bind to ABA-responsive elements (ABREs) on ABA-regulated genes. Notably, phosphorylation cascades like those signaling stomatal closure also lead to changes in ABA-regulated TFs. For instance, the ABA-responsive TFs ABF1 and ABF4 are activated upon their phosphorylation by ABA-inducible kinases CPK4 or CPK11 [111], as reviewed by Harrison et al [101].

On a similar line, preferential upregulation of JA pathway genes under salinity stress in barley plants has been reported [112]. Although the precise role of JA in drought and salinity remains unknown; it could be implicated as a molecule signaling cell death [102]. Nishiyama et al. [38], studying gene expression, concluded that exogenous ABA treatment strongly downregulated isopentenyltransferase (IPT), a key cytokinin biosynthetic pathway gene, but upregulated genes encoding cytokinin oxidases and dehydrogenases. Further, in addition to its well-documented role in controlling plant

growth and development in close associations with auxins and BRs [113], GA is also involved in cross-talk of hormonal interactions in signaling environmental inputs [114,115]. Various recent reports make it clear that interplay between environmentally activated ABA, ET, GA, and CK signals is crucial in determining plant stress responses [3,116,117].

There is evidence that some phytohormones also counteract adverse conditions. For example, a signal peptide system coupled with JA is reported to be involved in wound-induced salt-stress adaptation in tomato [118], indicating cross-tolerance signaling. The possible roles of phytohormones in abiotic stress tolerance and crosstalk between phytohormone signaling are illustrated in Fig. 2.

6. Recent attempts at deciphering the role of phytohormones in abiotic stress tolerance

6.1. Hormones help in pollen development under cold stress

Abiotic stress can affect any developmental stages, but the reproductive stage is perhaps most critical. If stresses are applied at the reproductive stage, it may damage the whole plant and ultimately reduce the crop yield. Further, among the various reproductive stages, pollen development is crucial and is affected by abiotic stresses such as drought, cold, and heat, leading to reduced crop yield [119]. In pollen development, pollen meiosis is the stage most sensitive to cold, which causes pollen sterility and also reduces anther dehiscence, pollen load to the stigma, pollen germination, and pollen tube growth [120,121]. Hormones such as GA and ABA are considered major signals for cold-induced pollen sterility and an understanding of molecular mechanism of pollen development under stress and non-stress conditions can be beneficial for hybrid seed production by producing novel sterile plants. In rice, Zhang and co-workers [122] developed a hybrid seed production line in the form of a new photoperiod-sensitive

genetic male sterile line by using transcription regulation of pollen development; for details, see review by Sharma [123].

6.2. Hormonal balance under cold stress

Kolaksazov et al. [124] reported that stress phytohormones such as ABA, JA, and SA trigger phosphoprotein cascade pathways, leading to expression of genes associated with cold stress tolerance. They reported high contents of JA in the three different populations at a controlled temperature of 22 °C, with a 10-fold reduction in sensitive plants but no change intolerant plants at 4 °C.

6.3. Salicylic acid increases germination, seedling growth, and enzymes activity

Gharib and Hegazi [125] showed that SA stimulated various growth aspects of bean seedlings, was responsible for biosynthesis of growth-promoting and -inhibiting substances, and reduced the adverse effect of cold stress in common bean. They conducted an experiment on six common bean varieties with optimal temperature 25 °C and chilling stress at 15 °C. They found that germination and seedling growth of the six varieties were slowed under chilling stress. Seeds treated with SA showed increased germination rate compared to untreated (control) seeds under control as well as chilling stress.

6.4. Hormone responsive protein mediated stress responses

In plant stress response, phytohormones play a vital role, and some proteins can be used for communication. Bhaskar et al. [126] reported that C1-(cysteine rich protein family) domain-containing proteins play a part in plant hormone-mediated stress responses. Authors identified 72 other proteins in *Arabidopsis* that contained all three unique signature domains. Transgenic lines also showed differential regulation of many abiotic stress-responsive distinct genes, indicating the

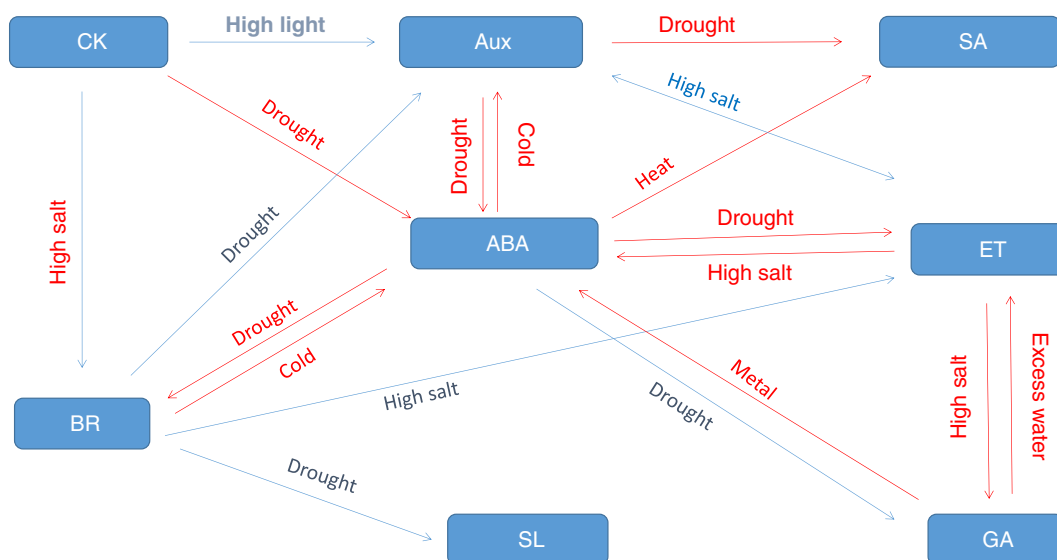


Fig. 2 – The possible roles of phytohormones in abiotic stress tolerance and crosstalk between phytohormone signaling

involvement of C1-clan protein family in hormone-mediated stress remediation.

6.5. Putative auxin efflux carrier involved in the drought stress response and drought tolerance

Auxin acts as a necessary signal in reaction to abiotic stresses. Zhang et al. [127] identified a putative auxin efflux carrier gene (*OsPIN3t*) in rice that acts in polar auxin transport involved in the drought response in rice. They also found that knockdown of the *OsPIN3t* gene leads to crown root abnormalities in the seedling stage and that its overexpression increased drought tolerance. Under 20% polyethylene glycol stress, GUS activity significantly increased under NAA treatment. The study showed that *OsPIN3t* is involved in auxin transport and the drought stress response in plants.

6.6. Phytohormones alleviate high-temperature stress

Owing to high temperatures, crop productivity is decreasing in many parts of the world. Chhabra et al. [128] performed an experiment to test the effect of various hormonal concentrations on heat-stress effects and observed that both growth-promoting and growth-retarding hormones mitigated heat-stress effects. They also reported that the most effective concentration of kinetin was $100 \mu\text{mol L}^{-1}$ followed by $50 \mu\text{mol L}^{-1}$ and that soaking seeds in ABA delayed 50% seedling mortality by 1 h and 50 min at 0.5 and $1.0 \mu\text{mol L}^{-1}$ concentrations.

7. Engineering phytohormones for producing abiotic-stress tolerant crop plants

7.1. Engineering techniques

Genetic engineering has opened new avenues for introducing abiotic stress tolerance in numerous economically important crop species. Recent success has made genetic engineering approaches as one of the most potent solutions for improving crop productivity under challenging environments. The success of transgenic research, however, depends largely on effective plant transformation methods for stable integration and functional expression of foreign genes in the plant genome. Since initial reports in tobacco [129,130], rapid developments in transformation technology have resulted in the genetic modification of large number of plant species [131].

Two general approaches are available for transferring gene(s) to plants: one vector-mediated, by a biological vector such as *Agrobacterium*, and the other direct gene transfer approach, where DNA is introduced into cells by physical, chemical, or even electrical means. Direct or nonbiological gene transfer methods include particle bombardment, DNA uptake into protoplasts in the presence of polyvalent cations, protoplast fusion with bacterial spheroplasts and with liposomes containing foreign DNA (lipofection), electrotransfection, polymer-based transfection (polyfection), silicon carbide fiber-mediated DNA uptake, injection-based methods (micro- and macro-injection), wave and beam-mediated transformation, desiccation-based transformation, and exogenous DNA application and imbibition

[131,132]. The use of biolistics or particle bombardment is by far the most widely used direct gene transfer method.

With its ever-increasing host range, *Agrobacterium tumefaciens* has become the clear method of choice for gene transfer to all of the main crop plants. This soil bacterium possesses the natural ability to deliver a distinct part of its plasmid DNA (transfer or T-DNA) into the nuclear genome of its host plant. This condition has arisen also partly because although direct gene transfer methods are useful for stable transformation as well as transient expression, there are still some problems: low frequency of stable transformation, unwanted genetic rearrangements due to the high copy number of genes, and the long period required to regenerate whole transgenic plants. In *Agrobacterium*, bacterial genes can be successfully replaced with gene(s) of interest, and interestingly, this replacement does not affect the transformation process or frequency [133,134].

For efficient transformation and subsequent regeneration, *Agrobacterium*-mediated methods are dependent on several factors. They are the choice of explant, the hormonal composition of the medium used, nutritional supplements, culture conditions before and during inoculation, duration of co-cultivation, virulence of the *Agrobacterium* strain, and concentration and composition of the bacteriostatic agent used. The length of selection and concentration of the antibiotic selection marker are also important. Other important factors are the plantcultivar and various conditions of tissue culture, including a robust system of plant regeneration [135]. However, through extensive efforts, remarkable progress has been achieved during the last 2–3 decades in plant genetic engineering. Optimized protocols have been developed for the *Agrobacterium*-mediated genetic transformation of a broad range of crop plants including monocots, previously considered to lie outside the *Agrobacterium* host range. Recently, success has been achieved in developing in planta transformation methods. However, inspired by the complex patent landscape of *Agrobacterium* technology and in search of a perfect (open source) platform for plant biotechnology, Broothaerts et al. [136] have identified three non-*Agrobacterium* species: *Rhizobium* sp. NGR234, *Sinorhizobium meliloti*, and *Mesorhizobium loti* as being capable of successful genetic transformation of different plant species. A recent addition to this list of biological vectors for genetic transformation of plants is virus-based vectors.

7.2. Metabolic engineering of phytohormones for conferring abiotic stress tolerance on crop plants

Considering that phytohormones are key regulators of plant growth and development as well as mediators of the response to environmental stress [24], hormone metabolism and signaling processes are excellent targets of manipulation to obtain enhanced abiotic stress tolerance. However, maintenance of hormonal balance to minimize possible adverse effects on growth and development is critical [15,137].

Among various phytohormones, ABA is perhaps the most sought-after hormone for engineering abiotic stress tolerance in crop plants owing to its identity as a stress hormone and its vast array of functions under environmental stress conditions, particularly drought. As a result, many of the key ABA biosynthetic pathway enzymes have been investigated transgenically for improved abiotic stress tolerance [138]. Park et al. [139]

reported enhanced osmotic stress tolerance by overexpressing an ABA-responsive stress-related gene in *Arabidopsis*. C-repeat binding factor (CBF) and/or dehydration-responsive element-binding (DREB) genes have been manipulated to confer improved drought tolerance. For example, overexpression of CBF1/

DREB1B from *Arabidopsis* improved tolerance to water-deficit stress in tomato [140]. Likewise, Al-Abed et al. [141] found expression of CBF/DREB genes under stress-inducible promoters in transgenic plants that do not express detectable levels of these genes under non-stress conditions, minimizing growth

Table 1 – List of attempts made at engineering phytohormones for enhanced abiotic stress tolerance of plants.

Item	Gene	Function of gene	Expression/ knock-out	Phenotype of transgenics	Reference
Plant hormone	MoCo sulfurase	Regulation of the last step of ABA biosynthesis	↑	Transgenic soybean showed higher biomass, yield, and overall enhanced drought tolerance	[150]
ABA	LOSS	Key regulator of ABA biosynthesis	↑	Transgenic maize with enhanced ABA accumulation and increased drought tolerance	[142]
	AtLOSS	Key regulator of ABA biosynthesis	↑	Increased salinity tolerance attributed to enhanced Na ⁺ efflux and H ⁺ influx and consequent	[151]
	NCED	Important role in rate limiting step of ABA biosynthesis for feedback control	↑	Increased levels of endogenous ABA, decreased stomatal conductance and increased drought tolerance	[152]
	MsZEP	Important role in ABA biosynthesis	↑	Heterologous expression of gene resulted in better salt and drought tolerance	[153]
	SnRK2.4	Important serine/threonine protein kinase in ABA signaling network	↑	Transgenic <i>Arabidopsis</i> exhibited enhanced tolerance to drought, salt, and freezing stress associated with decreased water loss, improved photosynthesis, and osmotic potential	[154]
Auxin	OsPIN3t	Auxin efflux carrier, important in polar auxin transport	↑	Increased drought tolerance in rice	[127]
	YUCCA6	Important gene in Auxin/IPA biosynthesis	↑	Overproduction of auxin attributed for increased tolerance to drought and oxidative stress	[27]
	YUCCA6	Important gene in Auxin/IPA biosynthesis	↑	Phenotypes of potato with higher auxin content and enhanced drought tolerance	[155]
	OsIAA6	A member of rice auxin/IAA gene family	↑	Better drought tolerance of transgenic rice plants via auxin biosynthesis regulation	[156]
	IPT	Cytokinin biosynthesis	↑	Transgenic tomato showed enhanced growth and yield under salt stress	[157]
Cytokinins			↑	Transgenic tobacco showed enhanced salt stress tolerance	[158]
	SlIPT3		↑	Transgenic tomato showed enhanced salinity stress tolerance	[159]
	CKX	Cytokinin dehydrogenase	↑	Transgenic <i>Arabidopsis</i> plants overexpressing cytokinin oxidase/dehydrogenase gene showed enhanced drought tolerance	[160]
	AtCKX1	Cytokinin dehydrogenase	↑	Transgenic barley plants showed better drought tolerance via better dehydration avoidance	[161]
	ERF-1 (<i>JERF1</i>)	Response factors for Ethylene as well as Jasmonates	↑	Rice plants showed increased drought tolerance	[162]
Ethylene	ETOL1		↑	Increased tolerance to drought and submergence	[163]
	ACC-Synthase	Catalyzes rate-limiting step in ethylene biosynthesis	Gene-silencing	Reduced ethylene levels with better drought tolerance in transgenic maize plants	[164]
	ZmARGOS	Negative regulators of ethylene signal transduction	↑	Improved drought tolerance of transgenic <i>Arabidopsis</i> and maize plants	[165]
	OsGSK1	BR negative regulator	Knockout of OsGSK1	Increased tolerance of knockout mutants to cold, heat, salt and drought stresses	[166]
Brassinosteroids	AtHSD1	Role in BR biosynthesis	↑	Overproduction of BR increased growth rate and seed yield, increased salinity tolerance	[167]
	BdBRI1	BR-receptor gene	Downregulation	Improved drought tolerance with dwarf phenotypes of purple false brome	[168]

↑: Overexpression

retardation and other adverse effects. Li et al. [142] overexpressed the *MoCo* sulfurase gene in soybean, resulting in higher biomass production and yield with overall enhanced drought tolerance attributed to higher ABA accumulation, reduced water loss through smaller openings of stomata, and induced antioxidant enzymatic machinery.

However, on some occasions, overexpression of gene(s) involved in ABA biosynthesis or catabolic pathways resulted in increased drought tolerance, but led to impaired growth due to pleiotropic effects even with the use of inducible promoters [143]. To offset these unwanted growth anomalies, Zhang et al. [122] overexpressed *CRK45*, a stress-inducible kinase involved in ABA signaling, and the resulting transgenics showed enhanced drought tolerance but with tighter control of ABA levels and signaling, indicating the role of *CRK45* in fine-tuning of ABA levels. Similarly, *IPT* was expressed under the control of stress-inducible promoters to avoid pleiotropic effects, leading to increased CK content, antioxidant scavenging, and better root growth with overall improved grain yield under drought conditions in *Agrostis stolonifera* [144,145].

Recently, transgenic poplars were produced via overexpression of the *Arabidopsis YUCCA6* gene (a member of the *YUCCA* family of flavinmonooxygenase-like proteins), which is involved in tryptophan-dependent IAA biosynthesis pathway and known to respond to environmental cues, under the control of the stress-inducible *SWPA2* promoter [27]. The transgenic lines displayed auxin-overproduction morphological phenotypes, including rapid shoot growth and retarded main root development with increased root hair formation. Also, SY plants had higher levels of free IAA and early auxin response gene transcripts. The transgenic lines showed tolerance to drought stress, associated with reduced levels of reactive oxygen species [27]. The rice mutant *CONSTITUTIVELY WILTED1* was deficient in the *YUCCA* homolog [146], and an activation tagline of *YUCCA7* in *Arabidopsis* showed enhanced drought tolerance [147]. Drought tolerance by overexpression of *AtYUC6* in potato was also observed in 4-month-old potted plants in greenhouses by monitoring recovery after withholding water for 18 days [148].

Sakamoto et al. [149] modified GA levels by overexpression of *OsGA2ox1*, a gene encoding GA2-oxidase. Interestingly, when the actin promoter constitutively expressed the gene, transgenic rice showed severe dwarfism but failed to set grain, given that GA is involved in both shoot elongation and reproductive development. In contrast, *OsGA2ox1* ectopic expression at the site of bioactive GA synthesis in shoots under the control of the promoter of a GA biosynthesis gene, *OsGA3ox2* (*D18*), resulted in a semi-dwarf phenotype showing normal flowering and grain development. Attempts at engineering phytohormones for enhanced abiotic stress tolerance of plants are listed in Table 1.

Given that biosynthetic pathways and convergence points for crosstalk are still not clear, there is further scope to increase our understanding in this regard and to identify novel genes encoding phytohormone metabolisms to be targeted for engineering abiotic stress tolerance in crop plants. Recent findings have opened various avenues for targeting phytohormones for genetic engineering to confer abiotic stress tolerance on important crop species.

8. Conclusion and future outlook

Overall, phytohormone engineering represents an important platform for abiotic stress tolerance, providing new opportunities to maintain sustainable crop production to feed the world under changing environmental conditions. It has a major application in plant stress tolerance and adaptation to a variety of stresses, owing to the involvement of multiple stress responsive genes. During the past few years, with the rapid development of genomic technology, much research has been performed towards understanding of plant abiotic stress response. Still many challenges are lying ahead to uncover and understand the complexity hidden in stress signal-transduction pathways. For example, to acquire wide-ranging understanding of plant responses to abiotic stress in coming years, more extensive work should be performed at the genetic level of the biosynthetic pathway of hormones such as IAA. Research to date indicates that phytohormone engineering has been initiated. The roles of plant hormones in responses to fluctuating environments have been demonstrated, and hormones play a primary role in determining plant stress responses. In this review, we have summarized the role of phytohormones, crosstalk among hormones, the importance of studying plant stresses in combination, and engineering techniques and strategies for developing stress tolerance in plants. In a wide range of stresses, plant hormones are involved directly or indirectly, and it is clear that plant hormones play roles in plant defense and plant-environment interactions.

In conclusion, although phytohormone engineering is promising for plant biologists, there is still a long way to go before the technology can reach its full potential. Among the greatest challenges that remain to be addressed is the development of stable phytohormone-engineered crops that produce main staple foods such as rice, wheat, and corn. Towards this goal, study should be focused on a combination of stress responses such as those in field environments, because different stresses are most likely to occur simultaneously under field conditions.

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