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ABA-Mediated Salinity and Drought Tolerance in Plants: Molecular and Physiological Perspectives

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Abstract

Abscisic acid (ABA) is a central regulator of plant responses to drought and salinity, integrating environmental signals with developmental and physiological adjustments. This review examines carotenoid-derived ABA biosynthesis, its turnover during stress recovery, and signal transduction through PYR/PYL/RCAR receptors, clade A PP2C phosphatases, SnRK2 kinases, and ABA-responsive transcription factors. We discuss the mechanistic basis of guard-cell ion transport and stomatal closure, stress-associated gene expression, osmotic adjustment, antioxidant regulation, and root growth responses. Particular attention is given to intersections between ABA and gibberellin or auxin pathways that coordinate seed germination and growth under water limitation. Evidence from different plant species demonstrates both the conservation and context dependence of these pathways. We critically evaluate limitations arising from developmental stage, genotype, stress duration, and trade-offs between water conservation and carbon assimilation. Translational prospects include tissue-specific manipulation of ABA signaling, chemical priming, and field-based evaluation of yield stability. A more precise understanding of ABA dynamics during stress and recovery will support durable crop improvement.

Keywords: Abscisic acid; Drought stress; Salinity stress; PYR/PYL/RCAR; SnRK2; Stomatal closure; Stress recovery

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Introduction

The amount of soil impacted by salinity is expanding due to global warming, and increasing sea levels [1]. Statistics show that around 6% (800 million hectares) of productive land worldwide becomes unusable due to high soil salinity [2]. Stress causes an imbalance in Earth's climate but also negatively impacts plant growth and physiological functioning [3]. According to estimates, salt stress lowers crop yields on 20% of globally irrigated land, causing losses of up to $12 B annually [4]. However, by the middle of the twenty-first century, salt will have destroyed half of the arable land. Salinity in the soil hinders root development, which delays plant growth and may even cause plant mortality [5]. In actuality, ion toxicity, osmotic stress,

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and nutritional deficiencies in plants are brought on by salt in the soil [6].

Furthermore, stomatal closure and membrane damage brought on by salt stress result in decreased carbon dioxide absorption, decreased hydrolase activity, and elevated lipid peroxidation levels [6]. These factors may trigger the production of many ROS, including O2−, H2O2, and OH− [7]. These substances may cause oxidative proteins damage to, lipids, DNA, and cell membranes. At the same time, they may cause MDA to accumulate, further interfering with the many metabolic and biological functions of plants [8]. To counteract the negative consequences of salt stress and to shield themselves from the negative properties of ROS, plants must have developed a variety of defense mechanisms [9]. An efficient tactic is the antioxidant defense system, which includes both antioxidants [10]. Low molecular weight substances like carotenoid are engaged in different cellular metabolic processes and serve as cofactors for different enzymes, eventually influencing the overall growth of plants [11]. The former primarily consists of antioxidants. It is true that the antioxidant defense system can successfully remove ROS and preserve the proper balance inside the cells [12]. Furthermore, two equally significant tactics that are essential to the foundation of cell composition and help to enhance salt tolerance are intracellular ion homeostasis (primarily K^+/Na^+) and the amalgamation and storage of suitable solutes such betaine and proline [13].

Conversely, a water shortage or dehydration stress causes the volume of the vacuole and the whole cell to shrink, while the concentration of internal solutes increases [14]. Turgor loss and plasmolysis result from a water potential imbalance that develops between the apoplast and symplast as dehydration worsens. Cell division and elongation are inhibited or growth is stopped if the impact is severe [15]. ROS, such as H_2O_2, O_2^-, $^1O_2$, are unavoidably formed in photosynthetic organisms and can cause serious oxidative damage [16]. Plant critical functions, including as photosynthesis, oxidative and electron transport chains, proton pumping, blooming, and normal development, are disrupted, which lowers crop output overall [17]. The degree of stress, the plant's genetic makeup, and its personal history determine whether a plant will survive or die. The distribution or reproductive success of species in a particular environment is determined by the cumulative effects of stress, and the growth and productivity of key agricultural species are ultimately governed by the synergism of various stressors [18]. Because they are sessile, higher plants have developed a great degree of flexibility to adapt to their constantly shifting surroundings [19]. Throughout their life cycle, they undergo continuous structural, physiological, and metabolic readjustments within the parameters of their genetic background, which contribute to their vigor and susceptibility to environmental stress [20]. Plants have progressed special ways to react to and adapt to their constantly shifting environments. They closely observe their surroundings and modify their metabolic processes to preserve homeostasis [21]. Therefore, the study of genome-environment interactions or the control of stress-inducible genes is important for considerate how plants react to external stimuli and for genetically modifying vulnerable plants to produce tolerance [22].

Nearly every crop that is significant to humankind is susceptible to elevated soil salinity levels. One of the most vital factor in farming is the amount of salt in the soil [23]. As a result, technology offers a quick and efficient way to produce salt-tolerant plant types while also boosting agricultural productivity and quality in saline areas [24]. Numerous researchers are now examining the mechanisms of salt tolerance and salt harm to plants. These researchers have demonstrated promising results by cloning many genes associated with salt tolerance and achieving great salt tolerance [24].

To enhance growth and better development, plants require oxygen, water, sunshine, and minerals, regulated by a number of internal variables in addition

to external ones [25]. Commonly known as "Phytohormones" or plant hormones. Originally, the word "hormone" was used strictly to describe secretory chemicals produced by specific glands, organs and tissues [26]. It is usually used to denote to the portable signals of living things and is presently often cast-off with a heading to describe the type of living things, plant hormones, insect hormones, etc [27]. All living things have hormones that are often unique to that species and represent the characteristics of its biological phenomena. The features of plant hormones are at least partially responsible for the unusual growth phenomenon known as developmental plasticity, in which a plant constantly creates new tissues and organs in its life cycle [28]. A group of organic, plant hormones has an impact on physiological processes when it is present in trace levels [29].

Plants contain very trace levels of chemicals known as plant hormones. They are derivatives of gases (ethylene), carotenoids (abscisic acid), adenine (cytokinins), terpenes (gabberellins), and indole (auxins) [30]. These hormones are produced in almost every part of the plant and are subsequently dispersed throughout the entire plant. Hormone functions can be antagonistic or gratis [31]. Hormones are decisive for processes including dormancy, seed germination, drought stress, and vernalization [32].

ABA controls dormancy and abscission and avoids plant growth. While commercially accessible synthesized ABA is a mixture, naturally occurring Abscisic acid is dextrorotatory (+) [33]. The phloem, xylem, and parenchyma cells are responsible for carrying ABA [34]. Between 1950 and 1960, scientists discovered ABA. [35] argued that although plant cells have endogenous hormones that support development, growth-inhibiting hormones that result in fruit senescence or abscission need to be regulated by other hormones, including ABA. abscisic acid just inhibits development; it doesn't cause abscission. The xanthophylls violaxanthin and neoxanthin are used in the synthesis of ABA. presence of epoxy-carotenoids, is necessary for the production of ABA [36]. However, the synthesis starts with IPP, which forms GGPP [37],which then forms Zeaxanthin and violaxanthin. Violaxanthin converts to cis-neoxanthin, and then cis-xanthin yields ABA. ABA is the result of aldehyde [38]. In addition to growing fruits and seeds, synthesis takes place in mature leaves and stems. Because environmental stressors like drought and waterlogging encourage the synthesis of ABA [39]. It is essential for abiotic stress tolerance. ABA reduces transpirational loss and persuades stomata to shut in response to extreme salinity and water stress [40]. ABA intermingles with other phyto-hormones, including nitric oxide, jasmonic acid, and signaling molecules, to promote stomatal closure [41].

Therefore, this chapter's core goal is to clarify the complex function that ABA plays in modulating plant responses to both these stresses by integrating a molecular and physiological investigation. In addition to coordinating physiological adaptations such stomatal control, osmolyte accumulation, and antioxidative defense, this chapter attempts to give a thorough grasp of how ABA affects stress perception, signal transduction, and gene expression. This work aims to highlight the importance of ABA in stress resilience, pinpoint important regulatory nodes within ABA-dependent pathways, and emphasize the implications of these discoveries for the creation of crop varieties that can withstand stress in the face of changing climate conditions by synthesizing current research.

ABA Biosynthesis and Metabolic Homeostasis

It has been proposed that several environmental cues, including light, either directly or indirectly control the synthesis of ABA [42]. However, salt stress and drought are the environmental factors that most significantly increase ABA biosynthesis Increased de novo biosynthesis is the primary cause of elevated ABA levels under various abiotic stressors [43]. Stress seems to inhibit ABA breakdown, whereas ABA and

stress alleviation seem to promote it [44]. Due to the fact that transcription inhibitors hinder stress-induced ABA production, drought and salt stress primarily cause ABA biosynthesis through transcriptional control of ABA biosynthesis genes [45]. The expression and control of ZEP, The ABA biosynthesis pathway's first cloned gene, have been closely examined in several plant species. ZEP genes were widely expressed throughout the plant, with leaves exhibiting the highest basal expression [46]. ZEP does not restrict ABA biosynthesis in photosynthetic tissues due to the amount of 9-cis-epoxy-carotenoid [47], in photosynthetic tissues like leaves are higher on a molar basis than the amount of ABA produced during stress [48]. The transcript levels of ZEP genes in the leaves of tomato and tobacco plants were also found to be diurnally measured, with up transcript levels during the day [49]. This could indicate that the circadian rhythm, rather than the plant's diurnal water potential changes periods, is in charge of regulating these transcript levels. There was no change in the amount of ZEP protein, even when transcript levels varied during the day. ZEP products' participation in the light-harvesting complex, rather than ZEP proteins' function in ABA biosynthesis, may be connected to the possible circadian control [50]. Since there are less epoxy carotenoid precursors in roots than in leaves, ZEP may restrict the production of ABA. ZEP genes in roots were evidently affected by drought stress, supporting this theory [51]. In both tomato and tobacco plants, its transcript levels multiplied many times following drought stress. various plant sections and developmental phases, as well as various plant species, may have distinct control of ABA biosynthesis genes [52]. The Arabidopsis ZEP gene exhibited a baseline transcript level in no stress circumstances, similar to that of the ZEP genes in tobacco and tomato [53]. However,[54] given that polyethylene glycol, salt, and drought increased the AtZEP gene's expression level in both the shoot and the root, it is clear that stress regulates this gene. The relative basal transcript levels may be partially responsible for the variation in ZEP gene regulation shown in various trials [55] as shown in figure 1. The genes' susceptibility to stress may be concealed by a high baseline transcript level. The expression of NCED genes has drawn special interest since it is thought that the cleavage stage in ABA biosynthesis is rate limiting [56]. It has been demonstrated that treatments including drought stress cause the expression of NCED in cowpea, avocado, tomato, maize, and Arabidopsis [57]. Within 15 to 30 minutes following leaf detachment treatment, there are noticeable increases in NCED transcript levels, suggesting that NCED gene activation can occur really quickly [58]. With the exception of AtSDR1, whose expression does not appear to be impacted by stress, drought and salt stress actually up-regulate all of the other ABA biosynthesis genes [59] as illustrated in figure 1. However, in the majority of these cases, their protein levels have not been investigated. Since ABA production does rise sharply in response to stress treatment [60]. AtAAO3 research, however, revealed that the protein levels of the protein did not alter in tandem with the transcript levels [61].

ABA Catabolism, Conjugation, and Stress Signal Termination

ABA accumulation reflects the balance among de novo biosynthesis, catabolism, conjugation, deconjugation, and transport, rather than biosynthesis alone. CYP707A family ABA 8'-hydroxylases initiate a major oxidative catabolic route, whereas UDP-glucosyltransferases form ABA-glucose ester (ABA-GE), a potentially reversible inactive storage form. β-Glucosidase-mediated ABA-GE hydrolysis can rapidly replenish an active ABA pool. Consequently, declining ABA after rewatering is not simply passive dilution: regulated turnover helps reopen stomata, restore gas exchange, and permit resumed growth. The relative contributions of oxidation, conjugate mobilization, and long-distance redistribution depend on tissue, species, and stress history [32]. A useful experimental

distinction is to measure ABA alongside ABA-GE and catabolites over both stress and recovery, rather than interpreting one endpoint hormone concentration as the entire response.

ABA Signal Perception and Transduction

Receptor Ligand Recognition and Activation of the Core Module

In the canonical ABA-dependent pathway, ABA binds the START-domain pocket of PYR/PYL/RCAR receptors and promotes conformational closure of a gate-and-latch arrangement. This enables the ligand-bound receptor to engage and inhibit clade A protein phosphatases 2C (PP2Cs), including ABI1, ABI2, and HAB1. In low-ABA conditions, PP2Cs limit activation of subclass III SNF1-related protein kinases 2 (SnRK2s); ABA-dependent PP2C inhibition releases this suppression and favors kinase activation. OST1/SnRK2.6 is particularly important in guard cells, whereas SnRK2.2 and SnRK2.3 contribute strongly to transcriptional and developmental responses. Activated kinases phosphorylate downstream ion channels and bZIP transcription factors, notably AREB/ABFs and ABI5 [69, 70, 72, 73]. Receptor isoforms differ in basal phosphatase inhibition, ligand affinity, expression, and oligomeric state, so the same endogenous ABA concentration need not produce identical responses in all tissues [70, 83].

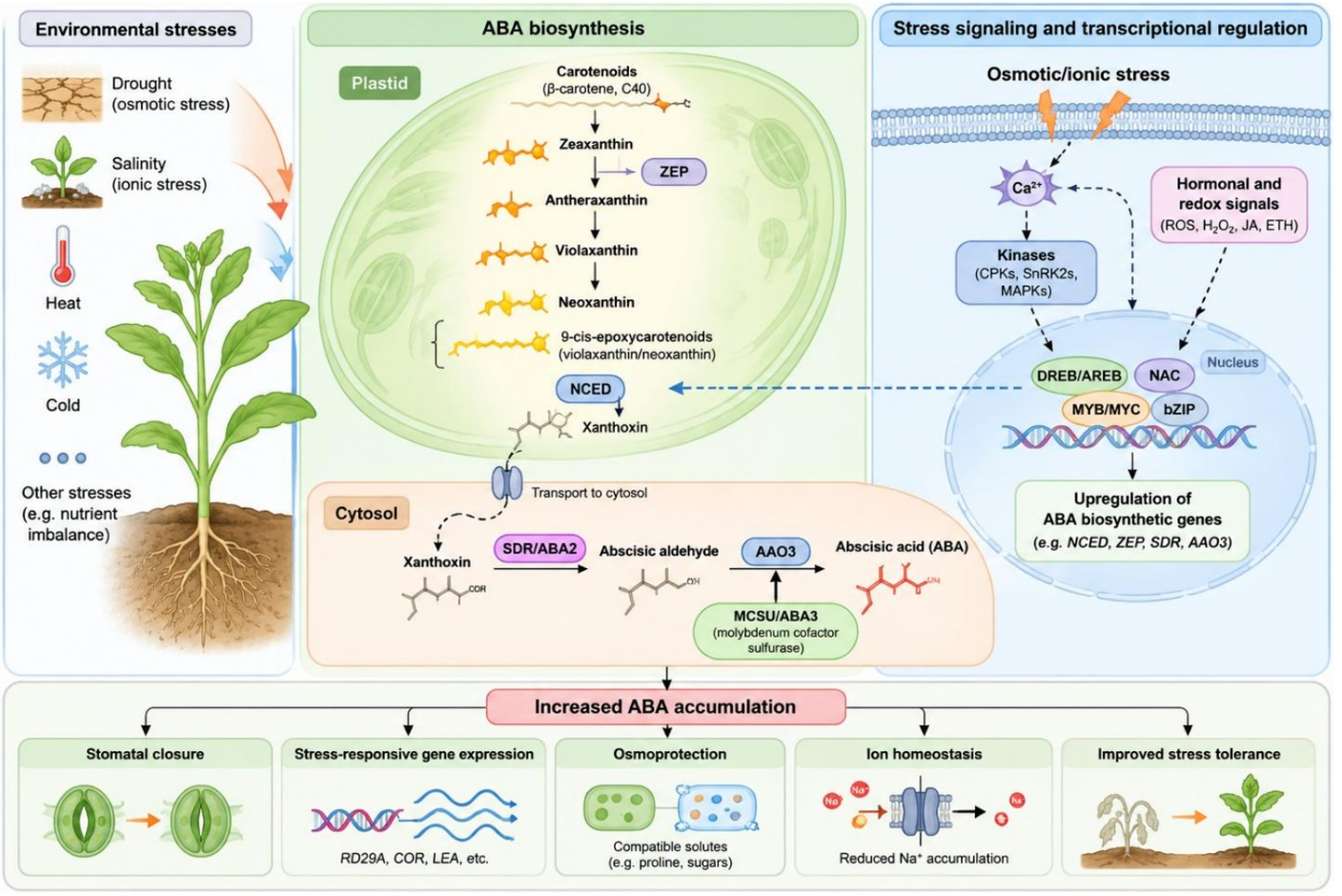


Figure 1. Schematic overview of abscisic acid (ABA) biosynthesis, stress-responsive signaling, and physiological adaptations in plants under abiotic stress. Environmental stresses, including drought, salinity, heat, cold, and nutrient imbalance, trigger interconnected signaling pathways that regulate ABA biosynthesis and plant stress

responses. ABA biosynthesis begins in plastids through the carotenoid pathway, involving the sequential formation of zeaxanthin, antheraxanthin, and violaxanthin, followed by the production of 9-cis-epoxycarotenoid precursors. Zeaxanthin epoxidase (ZEP) participates in carotenoid conversion, whereas 9-cis-epoxycarotenoid dioxygenase (NCED) catalyzes the oxidative cleavage of 9-cis-epoxycarotenoids to produce xanthoxin, a major regulatory step in ABA biosynthesis. Xanthoxin is subsequently transported into the cytosol, where short-chain dehydrogenase/reductase (SDR/ABA2) converts it into abscisic aldehyde. Abscisic aldehyde oxidase 3 (AAO3), supported by molybdenum cofactor sulfurase (MCSU/ABA3), catalyzes the final conversion to ABA. Stress-responsive signaling networks involving calcium (Ca^{2+}), reactive oxygen species (ROS), protein kinases, and transcription factors, including DREB, AREB/ABF, NAC, MYB/MYC, and bZIP proteins, contribute to the regulation of stress-responsive genes and ABA-associated pathways. Increased ABA accumulation coordinates multiple physiological and molecular adaptations, including stomatal closure, stress-responsive gene expression, osmotic adjustment, ion homeostasis, and cellular protection, thereby contributing to plant tolerance under adverse environmental conditions. This illustrates major established metabolic steps and representative regulatory interactions, which may vary depending on plant species, tissue type, developmental stage, and stress intensity. ABA, abscisic acid; ZEP, zeaxanthin epoxidase; NCED, 9-cis-epoxycarotenoid dioxygenase; SDR/ABA2, short-chain dehydrogenase/reductase ABA2; AAO3, abscisic aldehyde oxidase 3; MCSU/ABA3, molybdenum cofactor sulfurase; CPKs, calcium-dependent protein kinases; SnRK2s, SNF1-related protein kinases 2; MAPKs, mitogen-activated protein kinases; DREB, dehydration-responsive element-binding protein; AREB/ABF, ABA-responsive element-binding protein/factor; NAC, NAM/ATAF/CUC transcription factors; ROS, reactive oxygen species; JA, jasmonic acid; ETH, ethylene; LEA, late embryogenesis abundant proteins. ChatGPT (OpenAI, GPT-5.6 Sol) assist with the generation of this illustration.

Positive and Negative Regulators of Signal Output

Signal output is controlled by opposing activities: PYR/PYL/RCAR receptors and activated SnRK2s positively regulate downstream ABA responses, while clade A PP2Cs suppress their activity before receptor-mediated inhibition. ABF/AREB factors transduce kinase activity into changes in transcription, and feedback regulation can prevent persistent activation. The signaling circuit therefore functions as a tunable switch rather than an invariably beneficial stress-response amplifier. Excessive activation may conserve water at the expense of photosynthesis, whereas premature attenuation may increase dehydration risk [40, 43, 44, 69].

ABA is a vital phytohormone that is necessary for responding to many stress signals. Applying ABA to plants mimics the consequences of a stressful circumstance [62]. The pattern of stress gene expression overlap following cold, drought, excessive salt, or ABA administration because numerous abiotic stimuli eventually cause osmotic imbalance [63]. This implies that in order to preserve cellular homeostasis, ABA and other stress signals share components in the signaling pathway that interact with one another [44]. Numerous stress cues cause the induction of ABA levels. When the circumstances are favorable for seed development and growth, ABA really helps the seeds overcome the stressors and germinate only [64]. Additionally, ABA stops preterm embryos from germinating too soon. Since stomatal closure stops intracellular water loss during drought, ABA is a stress hormone [65].

ABA seems to have a major role in plant osmotic stress tolerance. For Several ABA-deficient mutants, including as aba1, aba2, and aba3, have been found in Arabidopsis [66]. There have also been reports of ABA-deficient tobacco, tomato, and maize mutants. These mutants develop similarly to plants of the natural type

when no stress treatment is applied [67]. If drought stress continues, ABA-deficient mutants will quickly wilt and perish. ABA-deficient mutants also exhibit poor development under salt stress. Freezing lenience, which also entails the activation of genes for desiccation tolerance, requires ABA [68].

According to Komatsu, Takezawa and Sakata [69] there are at least two ways that osmotic stress caused by dehydration or excessive salt is transferred: 1st is ABA-dependent, and the 2nd is ABA-independent. The main mechanism by which cold affects gene expression is an ABA-independent route. The presence of a cis-acting element known as the ABRE element is frequently necessary for ABA-induced expression [70]. According to Čajánek, Smite, Ivashchenko and Huranova [71], the components engaged in the signaling pathway may frequently cross talk or even converge, and there is no obvious distinction between both pathways. One good option that can mediate these cross-talks is calcium, which acts as a second messenger for different stressors [72]. Numerous studies have shown that ABA, drought, cold, and excessive salt cause plant cells' calcium levels to rise quickly.

Table 1: ABA Signaling positive and negative regulators

Signaling component	Inhibitors	Expressed
ABA Insensitive 1/2 (ABI1/2)	SnRK2	Tissues and developmental stages[73]
ABA Hypersensitive Germination 1 (AHG1)	ABA signaling	Predominantly in seeds and early seedlings [74]
HYPERSENSITIVE TO ABA 1/2 (HAB1/2)	SnRK2s	Guard cells and roots [75]
SRK2D/SnRK2.2 SRK2I/SnRK2.3		Seeds and vegetative tissues [76]
SRK2E/OST1/SnRK2.6		Expressed in guard [77]

Both regulation of the RD29A gene's transcript accumulation have been documented. Both signaling pathways have the ability to induce proline accumulation in plants [78]. According to [79], calcium plays a part in the ABA-dependent activation of the P5CS gene. It is known that the los5 mutant has decreased expression of the RD22, COR47, RD29A, COR15A, and P5CS genes as shown in figure 2. The transcriptional activation of a small number of stress-induced genes, represented by RD29A, is somewhat recognized, but this mechanism is not truly understood [80]. Phospholipase D, ABA, and calcium are also proposed to function as negative regulators of proline production in Arabidopsis [81]. Pea DNA helicase 45 (PDH45) transcript overexpression due to salinity stress followed an ABA-dependent pathway, whereas pea (CBL) and CBL-CIPK followed an ABA-independent pathway [82]. In general, the expression of genes related to osmotic stress is mostly influenced by ABA-dependent pathways [83]. It has recently been shown by [84] that plants may quickly adapt their ABA levels to shifting environmental signals by activating dormant ABA pools.

The relationship between ABA and the control of plant development is a complicated one. According to [85], under water stress, stress ABA regulates shoot growth and development. When xylem ABA is elevated due to soil dryness, shoot development may be hindered. However, more recent findings have demonstrated that shoot and root responses differ [86]. Sharp demonstrated that increased ABA buildup in roots is responsible for maintaining root development under low water potential [87]. They have demonstrated that ABA's function may entail preventing the synthesis of ethylene, a growth inhibitor under stress. Under conditions of water deprivation, [44] even proposed that stress ABA could be useful in maintaining some limited shoot and root development. It is reasonable to

propose that maintaining root development in conditions of water deprivation would improve drought resistance. The idea that ABA has two roles in its physiological control has been validated by more recent research [88]. When collected in significant quantities under stress, it inhibits activities like stomatal opening and plant growth expansion, hence aiding in plant survival [89]. It has been demonstrated that its stimulating function, at low concentrations and under more "normal" conditions, is crucial for growth in a number of organs, including the development of main roots and seedlings after germination [90]. [91] demonstrated that Arabidopsis has a short-chain dehydrogenase/reductase called SDR1 that catalyzes multiple steps from carotenoid-derived xanthoxin to abscisic aldehyde in the cytosol, which is involved in sugar sensing and signaling, which are crucial for many metabolic processes as well as for ABA synthesis [92]. Apart from osmotic stress, salinity also causes ion toxicity in plants due to excessive ion input without proper compartmentation and nutritional imbalances, which are frequently observed when potassium is replaced by sodium [93]. However, the primary harm to plants may be caused by internal osmotic stress when excessive salt intake led to high salt buildup in the intercellular gaps, or external osmotic stress caused by high ion meditations in the soil [94]. Plant responses to salt and water deficiency are tightly connected, with overlapping pathways, because the harm induced by salinity is primarily caused by changed water relations [95]. It is well known that plants exposed to salinity have a proportionate rise in ABA concentration, which is often connected with the water potential of the leaves or soil [96]. This suggests that salt-induced endogenous ABA is caused by a water deficit rather than a particular salt impact. According to [97], during salt stress, those with lower ABA levels are more adaptable. During germination, Arabidopsis mutants with lower ABA levels or sensitivity are more resilient to salt stress [98]. This is most likely because salt stress raises the wild type's ABA level, which inhibits germination. [99] found that *Brassica napus's* reduced ABA buildup under salt stress accounts for its greater salt tolerance when compared to the salt-sensitive *B. carinata*. Inhibition of leaf growth in many species is also associated with an increase in ABA concentration brought on by salinity. Although the degree of the reduction varies by genotype, recent research by [100] found a correlation between upsurges ABA concentration in the expansion zones of leaf and a decrease in the rate of leaf expansion. research revealed that using two rice cultivars that differed in their ability to withstand salinity revealed that the salt-tolerant lines naturally have lower ABA levels in their leaves [101]. Therefore, in many respects, ABA is essential to how whole plants react to salt and drought stressors.

Evolutionary Conservation and Diversification

Core elements of ABA biosynthesis and response are widely conserved among land plants, but their deployment varies across lineages. Bryophytes and vascular plants share several ABA-responsive stress-protection functions, while gene duplication and tissue specialization have diversified receptor, PP2C, and SnRK2 families in angiosperms. Comparative studies should distinguish conservation of protein components from conservation of specific downstream traits, especially stomatal responses and developmental programs. Differences among Arabidopsis, grasses, and woody or stress-adapted species caution against assuming that all ABA-associated traits transfer unchanged between crop backgrounds [37]. A comparative framework combining ortholog validation, cellular expression, and functional assays is more informative than sequence similarity alone.

Molecular and Physiological Mechanisms of ABA-Mediated Tolerance

Significant disturbances in cellular homeostasis occur in plants under drought and salinity stress, resulting in oxidative stress, ion toxicity, and water shortage [6].

When plant tissues, especially leaves and roots, rapidly increase ABA production in response to stress signals, a sequence of chemical reactions that promote stress tolerance are set off [102]. One of the most important aspects of ABA function is ABA-responsive gene expression. This is achieved through the activation of specific promoter elements in the genome known as ABA-responsive elements (ABREs). These cis-regulatory regions are detected and bound by a class of TFs known as the ABRE-binding/ABRE-binding factor (AREB/ABF) family [103]. These transcription factors play a crucial role in initiating the expression of downstream genes linked to dehydration tolerance, osmo-protection, and stress signaling. They belong to the group known as the basic leucine zipper (bZIP) [104]. ABA also induces other families of TFs such as DREBs, which operate through cross-talk with both ABA pathways. Furthermore, NAC TFs bearing the names NAM, ATAF, and CUC are essential for modifying gene expression in response to abiotic stressors; they frequently function in parallel pathways or downstream of ABA signaling [40]. Another essential function of ABA is the activation of antioxidant resistance mechanisms, which protect plant cells from the damaging effects of ROS [105]. Excessive ROS production during stressful situations can harm DNA, proteins, and lipids. Genes encoding antioxidant enzymes, are expressed more when ABA signaling is present [106]. Together, these enzymes scavenge ROS and preserve the cell's redox equilibrium. In addition to reducing oxidative damage, ABA's control of antioxidant systems preserves the integrity of cellular signaling throughout extended stress [107]. In order to preserve cellular structures during dehydration, ABA promotes the production of stress-associated proteins, including Late Embryogenesis Abundant (LEA) proteins and dehydrins [108]. Due to their high hydrophilia, LEA proteins build up in the cytoplasm and organelles when there is a water deficit. They work by keeping ion and water balance, avoiding denaturation and aggregation, and stabilizing proteins and membranes [109]. Particularly linked to defense against freezing and dehydration stress are dehydrins, a subclass of LEA proteins. ABA significantly induces their accumulation, which is thought to be a molecular indicator of plant stress response [110].

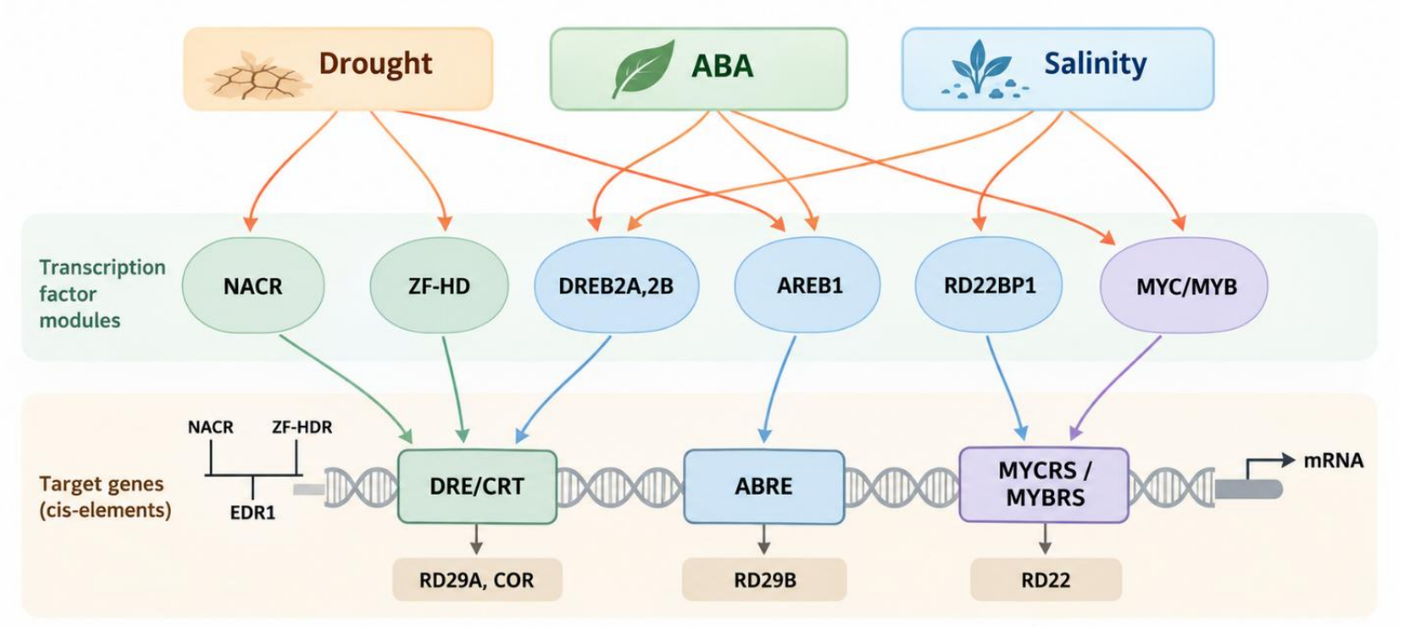


Figure 2. ABA-responsive transcriptional regulatory networks involved in plant responses to drought and salinity stress. The transcriptional regulatory networks activated by drought, salinity, and abscisic acid (ABA) signaling in

plants. Environmental stresses activate multiple transcription factor families, including NAC, zinc finger homeodomain (ZF-HD), dehydration-responsive element-binding proteins (DREB2A/2B), ABA-responsive element-binding protein 1 (AREB1), and MYC/MYB transcription factors. These regulators interact with specific cis-regulatory elements in the promoters of stress-responsive genes. DREB2A/2B primarily regulate ABA-independent transcriptional responses through dehydration-responsive element/C-repeat (DRE/CRT) motifs, activating genes such as RD29A and COR. In contrast, ABA-dependent signaling activates AREB/ABF transcription factors, which recognize ABA-responsive elements (ABREs) and regulate downstream genes, including RD29B. MYC/MYB transcription factors participate in the regulation of RD22 through their corresponding recognition sequences, whereas NAC and ZF-HD transcription factors contribute to dehydration-responsive gene regulation. Crosstalk between ABA-dependent and ABA-independent pathways coordinates stress-responsive gene expression and contributes to plant adaptation under drought and salinity conditions. The arrows illustrate representative regulatory relationships and do not necessarily indicate direct molecular interactions. ABA, abscisic acid; NAC, NAM/ATAF/CUC; ZF-HD, zinc finger homeodomain; DREB, dehydration-responsive element-binding protein; AREB1, ABA-responsive element-binding protein 1; ABRE, ABA-responsive element; DRE/CRT, dehydration-responsive element/C-repeat; MYC/MYB, MYC/MYB transcription factors; RD29A/RD29B, responsive to dehydration 29A/29B; RD22, responsive to dehydration 22; COR, cold-responsive genes; ERD1, early responsive to dehydration 1. ChatGPT (OpenAI, GPT-5.6 Sol) assist with the generation of this illustration.

Moreover, a composite network of protein phosphatases (PP2Cs), kinases (SnRK2s), and receptors (PYR/PYL/RCAR) closely regulates ABA signaling. In the absence of stress, PP2Cs block SnRK2 kinases, which stops ABA-responsive genes from activating [111]. ABA, on the other hand, binds to PYR/PYL receptors under stress, which block PP2Cs. This, in turn, releases SnRK2s, which phosphorylate and activate AREB/ABF transcription factors and other downstream effectors [112]. A quick and regulated transcriptional response to environmental stress signals is guaranteed by this key signaling mechanism.

Guard-Cell Signaling and Stomatal Closure

Water deficit and the osmotic phase of salinity induce ABA accumulation and signaling in guard cells. Receptor-mediated inhibition of PP2Cs permits OST1/SnRK2.6 activation, which promotes anion channel activity, particularly SLAC1, and contributes to suppression of inward-rectifying K+ uptake. ABA-linked reactive oxygen species and Ca2+ transients reinforce ion-channel regulation through partially overlapping routes. Anion efflux depolarizes the plasma membrane, favoring outward K+ movement; accompanying water efflux reduces guard-cell turgor and closes the stomatal pore. Physiologically this limits transpiration and protects leaf water status, although lower stomatal conductance restricts CO2 supply and can reduce carbon assimilation and yield under sustained stress [33, 44, 65]. The effect therefore depends on how rapidly stomata respond, how long closure persists, and whether conductance recovers after rewatering.

Transcriptional Programs, Osmoprotection, and Redox Balance

ABA-responsive elements (ABREs) are cis-regulatory DNA sequences bound by ABRE-binding proteins/factors (AREB/ABFs), which are activated by SnRK2-mediated phosphorylation. Their target programs include protective proteins, such as late embryogenesis abundant (LEA) proteins and dehydrins, and components involved in osmotic adjustment and redox homeostasis [66, 68]. Dehydration-responsive element binding factors (DREBs), by contrast, are prominently associated with

ABA-independent signaling, although substantial convergence occurs through shared targets and transcriptional regulators [37, 38]. It is important to distinguish an ABA-associated increase in antioxidant enzyme activity from direct proof of transcriptional regulation; tissue-specific genetic or biochemical tests are needed to support the latter [63–65].

ABA–Gibberellin Crosstalk

Through their interaction with ABA signaling, many hormones, including GA, control plants' ability to withstand abiotic stress (Figure 3) [41]. The amounts of two crucial hormones, ABA and GA, control the choice between germination and dormancy. Under conditions of cold, salt, and drought, GAs interact with other phytohormones to sustain growth and development [113]. DELLA proteins are known to control antagonistic interaction between GA and ABA. This technique helps plants resist extreme abiotic stresses by maintaining seed dormancy [114]. To shield seedlings from the damaging consequences of abiotic stressors, this crosstalk results in delayed germination. Abiotic stress conditions slow down the production of ABA Insensitive 5 (ABI5) [115], a basic leucine zipper transcription factor, which regulates ABA-responsive genes [116]. By controlling stress adaption genes like (LEA) genes under such circumstances, this growth suppression is accomplished. It is essential that LEA proteins be able to tolerate abiotic stresses as heat, drought, salt, and cold [117]. GAs, on the other hand, operate the other way. Under ideal circumstances, GAs accelerates seed germination. In order to facilitate effective germination, GAs inhibit ABA activity [118]. GAs control certain DELLA proteins, which disrupts ABA signaling and eliminates ABA's growth-diminution effects. Under abiotic stress conditions, ABA regulates certain DELLA proteins that decrease GA signaling to stop development [114]. The five DELLA proteins found in Arabidopsis are (GAI), (RGA), RGA-LIKE1 (RGL1), RGL2, and RGL3. The primary GA signaling repressor protein is RGL-2 [119]. Furthermore, Liu et al. (2016) demonstrated that the GA–ABA crosstalk-mediated seed-germination pathway is regulated by three Arabidopsis (NF-YC) homologs: NF-YC3, NF-YC4, and NF-YC9 [120]. They added that the DELLA protein RGL2 interacts with these NF-YCs. Additionally, the NF-YC–RGL2 complex regulates genes linked to germination and dormancy by targeting ABI5 [121]. Therefore, under abiotic stress circumstances, GA and ABA are essential phytohormones that determine whether seeds will germinate or go dormant.

Molecular Interface Between GA and ABA

ABA and gibberellins (GAs) impose opposing influences on dormancy, germination, and growth. GA perception through GID1 favors degradation of DELLA repressors, permitting growth-promoting transcriptional programs; a decrease in active GA can stabilize DELLAs and shift developmental responses toward restraint. ABA signaling through ABI5 and related transcriptional regulators reinforces dormancy and seedling protection. DELLA-linked interactions with transcriptional regulators provide molecular intersections rather than merely an inverse relationship between hormone concentrations [71, 73, 75]. In crops, the practical question is whether stress-protective restraint is sufficiently reversible to preserve establishment and biomass once favorable conditions return.

ABA–Auxin Crosstalk

Auxins and ABA function antagonistically to control plant cell growth, differentiation, pH, and calcium levels, among other developmental processes (Figure 3) [122]. For example, auxin and ABA antagonistically regulate a SHATTERPROOF-like gene that controls fruit ripening. ABRE-based transcription factor (ABI3) is auxin-regulated and has a significant function in controlling seed dormancy [72]. The interaction between auxin and ABA promotes seed survival under abiotic stress. ABA regulates auxin transport under water stress to sustain root development at the root tip [123]. It has been demonstrated that MYB96, an R2R3-type MYB transcription factor, modulates stress

tolerance under drought stress conditions by combining ABA and auxin signaling, which in turn regulates certain GH3 genes linked to auxin metabolism [124]. During salinity stress, two Cys2/His2 zinc-finger proteins, AZF1 and AZF2, have been shown to inhibit auxin-inducible and ABA-repressive genes, indicating regulatory interaction [125]. According to a recent study, WRKY46 controls auxin balance and ABA signaling to control lateral root growth under salt stress [126]. Furthermore, ascorbate peroxidase 6 (APX6) mediates crosstalk between ABA, auxin, and ROS, therefore shielding plants from abiotic stress [127]. Because of the interplay between these hormones, auxin-primed seed was discovered to have induced ABA activity, which saved plants from salt stress [128]. This interaction plays a significant part in enhancing the abiotic stress tolerance of both growing plants and seedlings [41].

Auxin Transport and Transcriptional Integration

The ABA–auxin relationship is not uniformly antagonistic: direction and outcome vary with organ, dose, and developmental context (Figure 3). ABA-dependent changes in auxin homeostasis and movement modify root branching, elongation, and hydrotropic responses. MYB96 connects drought-associated ABA responses to GH3-mediated auxin conjugation, whereas WRKY-type regulators have been implicated in the adjustment of root architecture under salt stress [77, 79, 81]. These intersections provide a plausible means of directing limited carbon and water resources toward root exploration, but greater root growth does not by itself demonstrate improved final yield. Comparative measurements of root traits, hormone profiles, water-use efficiency, and productivity are needed to define useful agronomic outcomes.

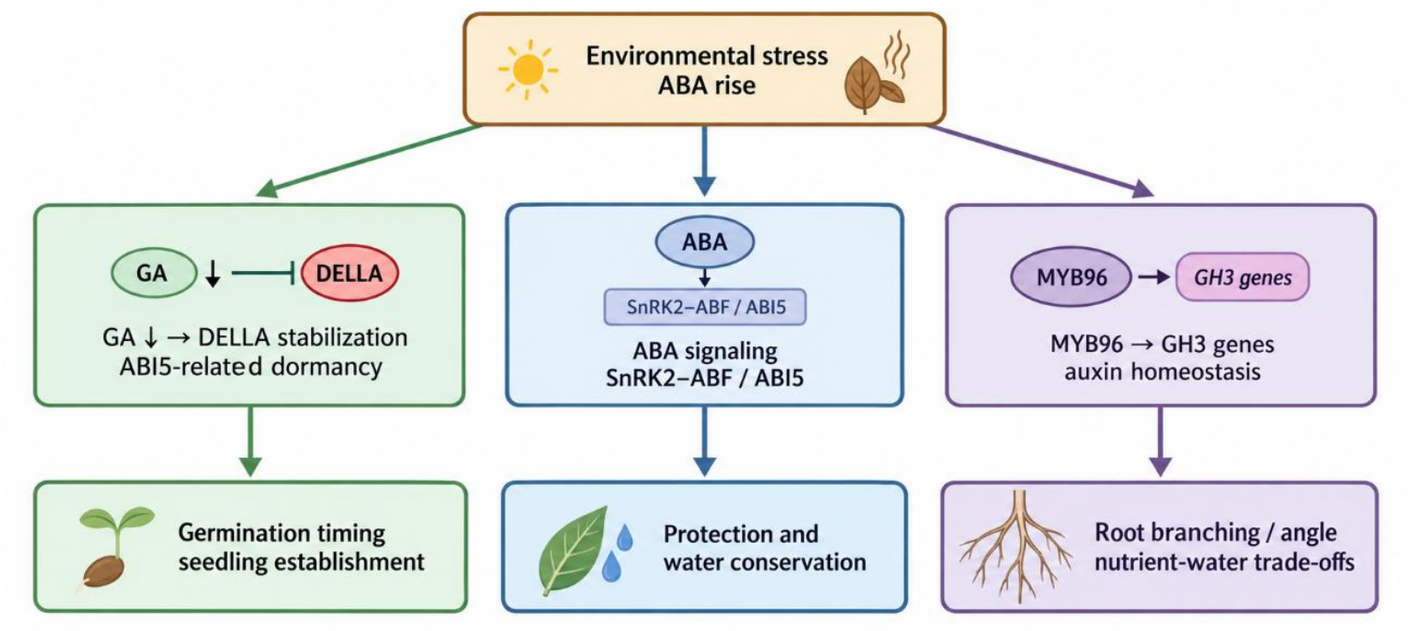


Figure 3. Molecular interactions between abscisic acid (ABA), gibberellins (GA), and auxin signaling pathways under environmental stress. The molecular interactions between ABA, gibberellins (GA), and auxin signaling pathways involved in coordinating plant growth, development, and stress adaptation. Environmental stresses, particularly drought and salinity, promote ABA accumulation and alter hormonal signaling networks. Reduced GA activity favors the stabilization of DELLA proteins, which act as negative regulators of GA-mediated growth responses and interact with ABA-associated regulatory pathways, including ABA INSENSITIVE 5 (ABI5), to

influence seed dormancy, germination timing, and seedling establishment. The ABA-dependent signaling pathway involves activation of SNF1-related protein kinases 2 (SnRK2s), which regulate ABA-responsive element-binding factors (ABFs) and ABI5, contributing to stress-responsive gene expression, cellular protection, and water conservation. Furthermore, ABA–auxin crosstalk involves the MYB96 transcription factor, which regulates GH3-associated auxin metabolism and contributes to auxin homeostasis and root developmental responses. These interconnected hormonal pathways influence root branching, root architecture, and the balance between nutrient acquisition, water uptake, and growth. Collectively, ABA–GA and ABA–auxin interactions coordinate developmental adjustments and physiological responses that contribute to plant adaptation under adverse environmental conditions. The illustrated relationships represent major regulatory interactions and may vary depending on plant species, developmental stage, and stress intensity. ABA, abscisic acid; GA, gibberellins; DELLA, DELLA-domain growth-repressing proteins; ABI5, abscisic acid insensitive 5; SnRK2, SNF1-related protein kinase 2; ABF, ABA-responsive element-binding factor; MYB96, MYB domain protein 96; GH3, Gretchen Hagen 3 family of auxin-responsive enzymes. ChatGPT (OpenAI, GPT-5.6 Sol) assist with the generation of this illustration.

Mechanistic Case Studies and Biological Significance

Structural and biochemical evidence has established that ABA perception by PYR/PYL/RCAR receptors promotes receptor–PP2C complex formation and inhibition of clade A PP2Cs. This releases SnRK2 kinases from suppression and activates downstream ABA-responsive transcriptional and physiological processes [69, 70]. Receptor oligomerization and kinase regulation influence ABA sensitivity, illustrating how structural insights can guide candidate interventions while requiring validation in relevant plant tissues and crop species [70, 83, 84].

Translational Applications and Agricultural Implications

Translation of ABA research into improved crops requires context-specific modulation rather than indiscriminate elevation of ABA signaling. Candidate strategies include seed priming and exogenous ABA treatment, receptor or PP2C allele selection, guard-cell-selective manipulation of kinases or ion channels, and genome editing of stress-inducible regulatory nodes [13, 35, 60, 88]. A useful breeding objective is not simply survival under severe experimental drought but improved yield stability during realistic intermittent water deficit or saline irrigation. Field validation should quantify canopy temperature, stomatal conductance, photosynthetic rate, phenology, grain or fruit yield, soil salinity, and post-stress recovery across environments and genetic backgrounds. Potential constraints include yield penalties, altered dormancy, delayed germination, and pleiotropic effects in roots and reproductive organs. Tissue-specific or inducible interventions may reduce such costs, but must be independently validated in field-relevant conditions.

8. Challenges, Growth–Yield Trade-offs, and Future Perspectives

Understanding functional genomics is essential to the effective development of salt and drought tolerance [129]. The structure and function of key genes involved in wheat plant development for drought resistance and, eventually, for increased grain production must be determined since drought resistance is a complicated feature [130]. With this information, plant biologists might apply genetic modification to change the structure and activities of certain genes [131].

The development of transgenic plants has not advanced as far, and there are several possible

explanations for this. Unwanted phenotypic traits like decreased plant growth and production can occasionally coexist with the survival rate [132]. It appears insufficient to produce salt and drought tolerance by altering a single gene. Although it is simpler to modify a single gene, it is less effective in conferring tolerance in different field situations. To govern the natural feedback control system and prevent the overabundance of intermediate products, several genes should be taken into account [133]. Furthermore, the change may result in whole new gene interactions that cause the genes to behave in ways that are not consistent with expectations. For more yield, adverse interactions between drought and salt tolerance as well as other features like photosynthetic rate must be taken into consideration [134]. For example, the maize HD-Zip I transcription factor ZmHB53 has been reported to enhance ABA sensitivity and seedling drought tolerance through effects involving the ABA receptor ZmPYL4 [135].

Molecular scientists tested transgenic plants in pots under water shortage for a few hours or days in many previous investigations [136]. The results showed that the plants' responses to injury or survival under extreme stress differed from those under long-term caused water deficiency stress over time. However, in natural settings, salt stress and water deficiency develop gradually as the soil dries up, and plants adapt their morphological and physiological characteristics appropriately, such as by accumulating osmolytes to keep their cells hydrated [137]. Experiments must thus be conducted under settings that are comparable to those in the field. Additionally, the length and severity of stress are important screening criteria that have been disregarded [138]. Transgenic lines failed to maintain the advantages seen in field trials under control conditions.

Critical Synthesis and Research Priorities

Three distinctions recur across the available evidence. First, ABA accumulation is an informative stress marker but not a sufficient predictor of tolerance: timing, cellular localization, receptor sensitivity, and catabolism can alter outcomes. Second, mechanistic demonstrations in model plants do not automatically establish improved yield in a crop field. Third, a protective response during peak stress can become maladaptive if stomatal reopening or growth recovery is delayed. Future research should prioritize time-resolved hormone measurements, cell-type-specific signaling analyses, genotype-by-environment experiments, and combined stress–recovery studies. These priorities connect molecular causality with agronomic benefit more convincingly than single-gene overexpression or acute seedling-survival assays alone [10, 22, 32, 56, 91].

Conclusion

Abscisic acid is a central coordinator of plant adaptation to drought and salinity because it couples environmental and hydraulic cues to metabolic regulation, gene expression, guard-cell movement, and developmental restraint. Its canonical PYR/PYL/RCAR–PP2C–SnRK2–AREB/ABF signaling module explains much of this integration, while ABA biosynthesis, conjugation, and catabolism determine signal timing and recovery. Protective processes include stomatal closure, osmotic adjustment, redox regulation, and accumulation of LEA proteins and dehydrins. Intersections with GA and auxin explain why stress tolerance is inseparable from germination, root architecture, and growth regulation. Yet a strong ABA response is not synonymous with greater crop productivity: extended stomatal closure and growth suppression can limit photosynthesis and yield. The next research priority is to connect tissue-resolved molecular mechanisms with reversible stress responses and field-tested improvements in water-

use efficiency, yield stability, and recovery under realistic combinations of drought and salinity.

Data availability

Not applicable

Acknowledgments

Not applicable

Conflict of interest

The authors declare that they have no conflict of interest.

Author Contribution

The authors confirm their contributions to the paper as follows: AA, MS: Conceptualization, writing—original draft preparation, and writing—review and editing. NS: writing—review and editing. MS, SF, HFB: Literature review, writing—review and editing. All authors have read and approved the final version of the manuscript and agree to be accountable for their contributions to the work.

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