Review Article

Abscisic Acid Mediated Abiotic Stress Tolerance in Plants

ABSTRACT

Abiotic stress is one of the major environmental stresses that decrease crop growth and yield even in irrigated soils worldwide. An important plant hormone abscisic acid (ABA) plays a vital role in addressing various stresses, such as thermal or heat stress, high salinity level, heavy metal stress, low temperature, drought, and stress on radiation. Its role is well explained in different processes for development, including germination of seed, stomata closure, and dormancy. Abscisic acid works through alteration of the gene expression levels and subsequently analyzing the cis and trans-regulatory components for receptive promoters. It is considered to have an interaction with the signalling elements of processes taking part in stress response and seed development. In general, a plant can be vulnerable or tolerant to stress when the correlated actions of different stress-reacting genes are taken into account. Many transcription factors are required for the regulation of expression of abscisic acid-responsive genes through interacting with their specific cis-acting components. Therefore, the mechanism behind it should be understood to make the plants stress-tolerant. This review explains the significance and function of ABA signaling concerning specific stress, the management of abscisic acid biosynthesis, and transcription factors (TFs) associated with stress tolerance.

Keywords: Abscisic Acid; abiotic stress; drought stress; heavy metal stress; water stress; seed germination

1. INTRODUCTION

Several processes promote plant development and growth. The phytohormones govern such processes continuously. One of the phytohormones is abscisic acid, which controls a number of plant development and growth attributes, like removal of the leaf, fruit maturity inhibition, among others~~and so on~~. Abscisic acid is often referred to as the stress hormone, which respond to various stresses of the environment, including abiotic ~~stresses as well as~~and biotic stresses [1]. Wani et al. [2] discussed analytically ~~analytically discussed~~ the significance of all major~~main~~ phytohormones in plant nutrition~~nourishment~~ and growth, the tolerance of abiotic stresses, and techniques providing abiotic stress tolerance in plants.

Abscisic acid~~, a small molecule,~~ is categorized as a sesquiterpenic~~sesquiterpene~~. It is non-planar and possesses many useful moieties. During the drying process, the production of abscisic acid occurs, and breakdown occurs when there is desiccation Drying? Desiccation? I did not understand this sentence. [3]. ABA appears in the roots of the plant as well as in end buds at the tip of the plant. C-15 abscisic acid framework is usually present in predecessors for the biosynthetic process, including xanthoxin, phaseic acid, abscisic alcohol, 8-hydroxy-ABA, dihydrophaseic acid, and abscisic aldehyde. Several stress signals in the plant system elicit the endogenous level of ABA produced. These involve the reinforcement of genes that encode β-carotene ABA enzymes [4]. Sorry, but I can't understand this paragraph. I believe authors can look for more specific articles to describe and explain the role of ABA

ABA plays a significant part in multiple cell-based mechanisms such as vegetative growth, seed production, germination and development of seeds, and ecological stress response [5].~~ Aiming to get dissolve in boiling water without degradation~~ (I did not understand ….), ABA is stable at high temperatures [1]. It performs various cell-level functions that include controlling the production of the enzymes needed to protect cells from desiccation [6,7], high temperature stress, and further mechanisms, such as movement of water [8,9] and iron metabolism. Xiong and Zhu [5] suggested that in general, plant reaction to changes in microclimate parameters like radiation, moisture, and temperature could be regulated by making modifications in abscisic acid concentration. Increased ABA quantities are helpful during cold resistance. In bean plants, such an increase in ABA levels was observed when introduced to short duration thermal stress [10]. At the time when the need for CO_2 is small or in water scarcity conditions where the plant cannot sustain much water loss through transpiration, ABA is involved in the stomata closure process. Therefore, abscisic acid is renowned at an organ level for a significant role in stomatal movement [8,11], in the development of shoot and root, and tissue hydraulic movement [9,12]. Abscisic acid is considered to be a possible applicant at plant level concerning water/salt stress and the relation with multiple signals derived by the plant for the contact between roots and shoots, however also for communicating with certain plant signals relating to organ-to-organ contact. ABA imparts an essential role in inhibiting seed germination. The mechanism of seed germination is supposed to be stopped after putting in the field.

~~While abscisic acid is best found in a large number of pH levels, it changes into γ-Lactone in a purely acidic environment like hydrochloric acid [13]. The carboxy-group is present in the side chain as a weak acid. The lipophilic character of abscisic acid, therefore, depends heavily on pH and promotes high lipophilic content at lower pH levels.~~(???) Different internal and external (environmental) signals regulate plant ~~nourishment~~ nutrition and growth. For instance, in plants depleted of minerals and nitrogen, the ABA content is increased [5]. ~~Abscisic acid is photosensitive to the side chain of dienoic acid and the ring enone. 2-trans-abscisic acid (2E-ABA) form of abscisic acid is inert from a biological point of view [14]~~(???). Leaving aside the information on nutrition and growth, how important is the other information in this paragraph?

I suggest that the authors further develop the topic of nutrition and growth versus ABA. And finish the Introduction by explaining the importance of the study, what it presents again, what are the objectives of the review

2. BIOSYNTHESIS OF ABSCISIC ACID

ABA is an isoprenoid or terpenoid metabolite form. Isopentenyl (IDP) is a precursor molecule of C5 (five-carbon) from which it is developed. IDP was initially considered, in some eubacteria initially, and eventually in high plants [15] that every single isoprenoid is made from mevalonate (MVA) till lately a subordinate channel been spotted for the production of isopentenyl. Different enzymes that use β-carotene to produce abscisic acid are involved. Abscisic acid was recognized as well as isolated from the cotton balls in 1960. A number of plant cultivars can synthesize abscisic acid mutants. The identification and physiochemical properties of these mutants have ameliorated our understanding of the biosynthetic channel in several plant species.

Many enzyme-catalyzed steps mediate the conversion of β-carotene to abscisic acid (Figure 1). Another possible factor in calcium-dependent phosphorylation can be the abiotic stress caused by the triggering of a range of biosynthetic ABA genes correlating to zeaxanthin oxidases, 9-cys-epoxycarotenoid dioxygenase, Abscisic acid-aldehyde oxidase, and molybdenum cofactor sulfurase (MCSU) [16]. Zeaxanthin, a trans-isomer form, is synthesized by all-*trans*-lycopene hydroxylation through carotene. The primary stage comprises a synthesis of CIS-isomers of violaxanthin and neoxanthin, each with a split to create the ABA predecessor C15 (Figure 1). Nonetheless of the verification that abscisic acid has fifteen atoms of carbon, ABA does not emanate instantly from the C15 sesquiterpene predecessor, farnesyl-diphosphate in plant species. Regardless, ABA emerges from the MEP (2-C-methyl-d-erythritol-four-phosphate) path through the cleavage of C40 carotenoids [15].

~~Zeaxanthinepoxidase~~Zeaxanthin epoxidase (ZEP) has a catalytic effect on the formation of violaxanthin. Principally, the ZEP gene was cloned in ***Nicotiana plumbaginifolia*** via insertional mutagenesis. This ZEP gene codes for a protein with a ferredoxin-resembling sequence that needs

FAD-binding monooxygenases [15]. The following genes are activated in seeds for abscisic acid accumulation and biosynthesis. In some situations, expression of NtZEP exceeds a maximal of 1/3rd to 1/2nd of seed development phases and is connected to the accumulation of ABA over that time period [5]. In an immoderate mild environment (I did not understand? The environment can best be described), an opposite response is observed to be catalyzed by the help of violaxanthin de-epoxidase (VDE) in the chloroplast. Two enzymes, one neoxanthin synthase, and the other isomerase could play a role in the development of neoxanthin and violaxanthin cis-isomers. A family of the 9-cis-epoxycarotenoid dioxygenases (NCED) catalyzes cis-xanthophylls cleavage [17]. The maize vp14 mutant was used to suppress the ZmNCED gene [18]. Later, short-chain alcohol dehydrogenase (ABA2) is used to modify xanthoxin and to generate abscisic aldehyde. The last stage in the abscisic acid biosynthesis pathway is the abscisic aldehyde oxidation into carboxylic acid by an abscisic aldehyde oxidase. The abscisic aldehyde oxidase protein consists of MoCosulfurase-activated molybdenum co-factors.

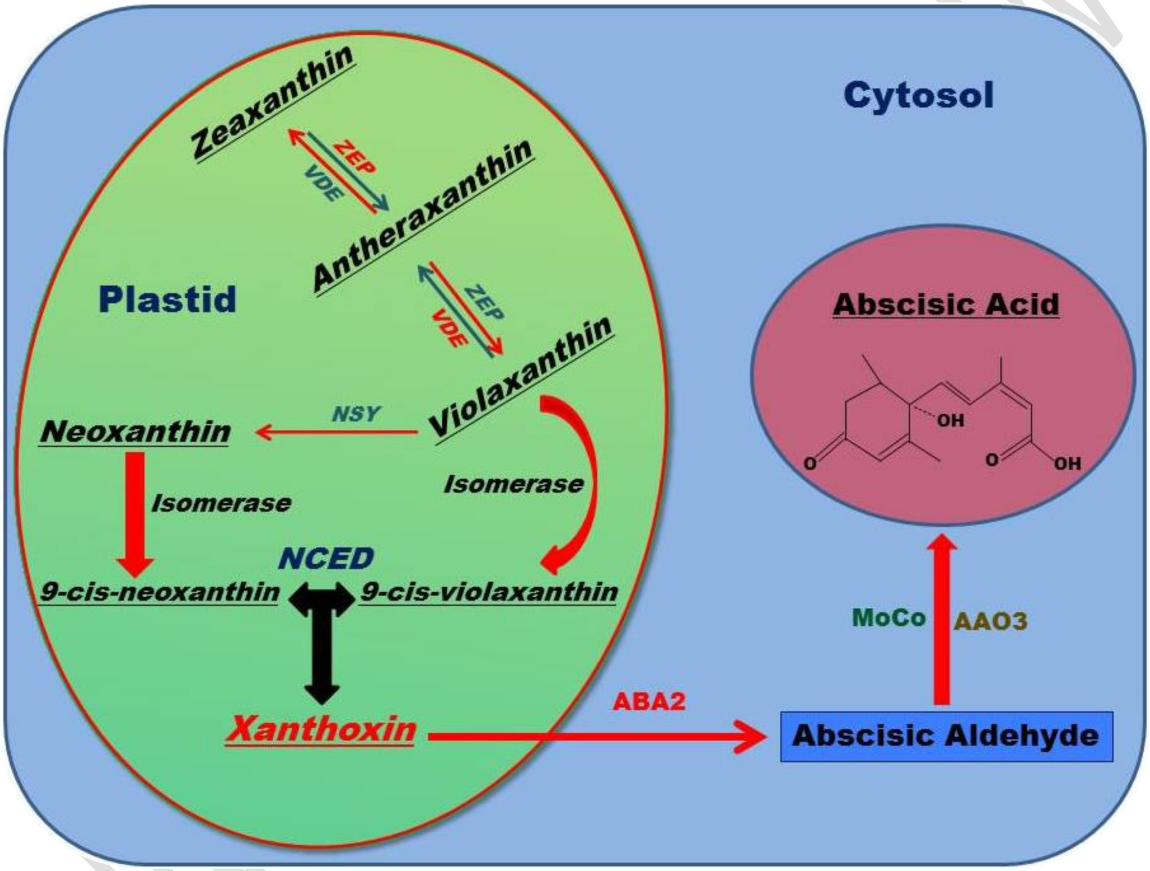

Figure 1: A general framework of Abscisic acid biosynthesis in plants

Neoxanthin and violaxanthin cis-isomers are cleaved by ~~nine~~9-cis-epoxycarotenoid dioxygenase (NCED) enzymes to form C-25 metabolite, xanthoxin, and C15 product (Figure 1). Insertional mutagenesis was utilized to clone the NCED gene (VP14) in corn for the first time [19].

The biologic functional configuration of cis-xanthotoxin abscisic acid requires two stages that are catalyzed by enzymes with an intermediate abscisic aldehyde (Figure 1). Up to now, only in *Arabidopsis* alone, the genes have been located for such enzymes. AtABA2 activates the metamorphosis of xanthotoxin to abscisic aldehyde. AtABA2 is included in the SDR family. Map-based cloning [20,21] through isolated *Arabidopsis* mutant alleles from several genetic screens is used to identify AtABA2 [15,21].

Mutants deficient in abscisic acid production play a significant role in understanding the ABA biosynthesis pathway. ~~Mutants that lack abscisic acid impart a significant function in exhibiting the ABA~~

~~biosynthesis pathway~~. On the basis of wilty (???) appearance and advanced seed germination, like in barley, tobacco, *Arabidopsis*, tomato, potato, and maize, these mutants can be examined [1]. Until the biological functions of the defective genes were understood, profiling feeding assays and abscisic acid biosynthetic intermediates using such mutants showed a specific mechanism for ABA biosynthesis. The catabolism activity and hormone’s rate of biosynthesis predict the concentration of abscisic acid in particular tissues of plants. Thus, if we identify all the genes participating in ABA biosynthesis, it will help us understand the role of plant hormones in directing development and growth.

3. ABA BIOSYNTHESIS CONTROL BY WAY OF ABIOTIC STRESS

The increase in abiotic stress enhances the ~~*de novo*~~ biosynthesis of abscisic acid. It is aroused by stress relief and is essential in hampering its degradation. ZEP gene plays a vital role in abscisic acid biosynthesis and is expressed and cloned in a wide variety of plants.

This gene is present in all plant portions and is somewhat correlated with leaf expression [22]. Besides, the abscisic acid biosynthesis level via the ZEP gene is controlled in many parts of the plant and cycles of growth and also in specific plant species. In non-stress conditions, the ZEP gene has a similar level of the basal transcription ***Arabidopsis*** as that in tomato or tobacco. The changes in ZEP gene expression are partially linked to basal levels of the transcript that assure gene stress inducibility as determined in several experiments. Still, there is less debate regarding another expression of ABA biosynthesis genes (AtSDR, MCSU, AtAAO3, and NCED). After cleavage in the rate-limiting stage, ABA biosynthesis is achieved, and therefore, the NCED gene expression is essential. In water deficient conditions, it is observed that NCED genes are overexpressed in avocado [23], maize [18], *Arabidopsis* [24], tomato [25], cowpea [26], and bean [27]. After 20–35 minutes of the leaf disentanglement or mediated desiccation, a significant increase in NCED transcript rates have been recorded [5], offering proof that NCED genes are triggered instantly. Because the process of ABA biosynthesis rises significantly in reaction to stress, it is concluded that protein concentrations in the associated genes enhance with the levels of the transcript that were also found in the NCED gene [5].

The final outcome of the biosynthesis process, ABA, pessimistically (???????? Why?) controls the assembling of ABA through the activation of catabolic enzymes [28]. ABA 8′-hydroxylase activity and cytochrome P450 enzyme activity cause the breakdown of ABA. This degradation of abscisic acid is controlled by exogenous aggregation of abscisic acid. Since the NCED gene product controls the rate-restricting phase in the abscisic acid biosynthetic pathway, the knowledge concerning the auto-regulation of ABA biosynthesis of the gene product is quite finite. The exogenous abscisic acid does not affect the NCED gene in cowpea and tomato [26,29]. This may then be deduced that abscisic acid is not able to increase production, but can degrade it.

9-cis-epoxycarotenoid dioxygenase (NCED1) catalyzes the initial stage of the abscisic acid biosynthesis pathway and expands substantially in grapes [30]. The final result is an aggregation of ABA in different tissues that eventually induce berry growth and maturation [31]. Where's the stress?

In *Arabidopsis*, abscisic acid up-regulates stress-stimulated ZEP, AAO3, and MCSU [5]. Exogenic abscisic acid controls the expression of these genes. However, the production and degradation of ABA biosynthesis are more important to regulate the abscisic acid expression and adapt development strategies and stress response in plants. Since ABRE- and DRE-like cis components are promoters of stress-inducing abscisic acid genes [32,33], such genes are therefore regulated similarly as the stress-responsive gene class CRT/DRE [34]. Through the production of reactive oxygen species (ROS) messengers are induced by abscisic acid to trigger defense responses [35]. Besides, the abscisic acid signal activation pathway stimulates the function of antioxidant enzyme genes and non-enzymatic defense system genes [36].

The screening may be performed in vegetative tissues with the aid of ABA in stress reaction conditions. It will undoubtedly help to classify new loci necessary for the control of ABA metabolism [1]. ABA has different categories of activities that include diverse regulatory processes, processing, transduction, signal interpretation, and deterioration. Evaluating the crucial role of abscisic acid in plant stress and its management system will assist in designing concurrent methods for producing or genetically regulating plants with widespread environmental resistance.

4. ABIOTIC STRESS and ABSCISIC ACID SIGNALLING

The phytohormone abscisic acid has high significance in the development of mechanism, and vigorous stress response to environmental stimulus (Table 1). The plant experiences certain abiotic stresses including high salt concentration (salinity), extreme temperature (cold or heat~~freezing or boiling~~), and drought [37]. The plants utilize abscisic acid to imitate stress and alter ABA phases by modifying environmental and physiological conditions relative to seed dormancy and germination delays, progressive seed development, stimulation of stomatal conductance, leaf senescence, the synthesis of lipids and proteins, protection from pathogens and embryo development [16].

Table 1: Description of ABA mediated abiotic stress responses in various plant species

Sr. No.	Stress	Plant studied	Plant organ	Applied dose	Impact	References
1	Cold	Summer Squash	Fruit	0.5 Mm	Increased expression of genes involved in ABA ~~signalling~~signaling	Carvajal et al., 2017
2	Drought	Tea Plant	Leaves	50 mgL^{-1}	Stimulation of lipid metabolism and flavonoid biosynthesis	Gai et al., 2020
3	Drought	Cotton	Leaves	0.5 μmolL^{-1}	Stimulate enzymatic anti-oxidant system and ROS scavenging activity	Hu et al., 2021
4	Drought	*Aristoteliachilensis*	Endogenous ABA determination		Increased anthocyanin level	Gonzalez-Villagra et al., 2018
5	Salinity	Rice	Inoculation with ABA-producing endophytic bacteria		Up-regulation of glutamic acid, proline and salicylic acid	Shahzad et al., 2017
6	Salinity	Wheat	Root	0, 5, and 10 μM	Reduced transpirational flow and Na^{+} uptake, up-regulation of anti-oxidant mechanism	Parveen et al., 2021
7	Heat	Rice	Leaves	1, 10 and 100 μmol L^{-1}	Higher expression of heat shock proteins and ROS scavenging activity	Rezaul et al., 2018
8	Heat	Wheat and spelt	Seed	10—7 M 10—6 M	Improvement in overall growth	Kosakivska et al., 2019
9	Hypoxia	Rice	-	50 μM	Stimulated proline biosynthesis and antioxidant scavenging activity	Cao et al., 2020
10	Flooding	Soybean	-	10 μM	Improved transcriptional responses	Yin et al., 2017

11	Flooding	Rice	Root	-	Formation of radial oxygen loss (ROL) barrier	Shiono et al., 2021
12	Cu toxicity	*Artemisia annua*	Root	100 µM	Enhanced artemisinin biosynthesis and ROS scavenging activity	Zehra et al., 2020
13	Cadmium toxicity	Mungbean	Leaves	5, 10 and 15 µM	Improved physio-chemical and ROS scavenging activity	Leng et al., 2020
14	Zn toxicity	Wheat	Seed	10 µM	Improvement in overall growth	Vasyuk et al., 2019
15	Zn toxicity	*Arabidopsis thaliana*	Seed	ABA mutants of *Arabidopsis thaliana*	Improvement in physiological responses	Li and Song, 2020

Environmental stress exposure, as with drought, can have adverse effects on plant growth and vegetation production (Table 1). Abiotic stress is harmful environmental stress that affects crop yield and plant development globally [38]. In general, stress is a multi-faceted process that takes place at the time of plant growth. The rate of plant metabolism and the stress level drives various responses of plants. It has been shown in a review by Tuteja [16] that until the end of the signaling pathway, ABA metabolome activity and stress signals affect cellular homeostasis. Moreover, osmotic imbalance and cell desiccation is generated by additional abiotic stresses. Rizwan et al. [39] investigated the use of endogenous and exogenous ABA modifications to make plants tolerant to metal stress; enhanced plant development, improved gas exchange features, increased photosynthetic pigments, and enhanced biomass.

In response to a specific stress, a hormonal change is observed that includes the rise of leaf ABA and reduction in cytokinins. Several leaf ABA responses contribute to cell wall expansion, hydraulic conductance of roots, and tissue turgor in some plants (Table 1). Decreased carbon intake will lead to the accumulation of carbohydrates and inhibit photosynthesis to combat the minimum carbohydrate requirement of the plant. The key reason for photosynthesis arrest of ABA contributes to lowered stomatal conductance and photosynthesis inhibition due to reduced photosynthetic enzymes concentration and carbohydrate aggregation [40].

5. HEAVY METAL STRESS

The main contaminators of nature are heavy metals. In cultivated agricultural lands, concentrations of certain heavy metals ~~like~~ such as chromium, lead, cadmium, mercury, and copper are much higher due to mankind interference [41]. Heavy metal exposure is the key source of abiotic stress, causing harmful health effects to people, plants, and animals [42-45]. Being highly reactive, heavy metals have an adverse effect on the synthesis of energy, senescence, and growth processes.

It appears to be accurate that ABA influences many developmental and physiological stages. In several plant species, ABA significantly improves freezing, drought, chilling, and salt resistance [46,47]. Heavy metals like Zn, Cd, Al, and Ni [48] increase the concentration of abscisic acid in plants (Table 1). Cadmium, a divalent cation, is a toxic heavy metal [49]. Cadmium (Cd) leakage in air, soil, and water usually occur as excretion from mining, burning, and waste drainage industries, fertilizers, and sewage sludge. ~~Flora (?????), leading to deadly signs like limited growth, can easily take it up [50].~~ Cadmium affects photosynthesis in plants [51], prevents stoma opening [1], and reduces chlorophyll content [52]. It was seen that the plant roots had acquired the cadmium-generated abscisic acid. However, it was not identified in ***Typha*** and ***Phragmites*** shoots (Table 1 Where in table 1 is this information?).

In Taiwan, the rice crop showed resistance against cadmium [47]. ABA is associated with Cd resistance at higher temperatures (32/37°C) in rice seedlings (Table 1). The result was based on the observation that (1) By comparing the extent of exogenous abscisic acid in the cadmium sensitive variety (TN1) and the cadmium tolerant variety (TNG67), an increase was observed in the cadmium tolerance of TNG67; (2) when an external dose of abscisic acid was provided, cadmium tolerance of TN1 was enhanced; (3) While the application of fluridone decreased ABA content and TNG67 seedlings Cd tolerance level; and (4) the re-application of abscisic acid to TNG67 seedlings has reinforced the fluridone impact on cadmium toxicity. These findings reveal that controlling abscisic acid biosynthesis endogenous levels may lower cadmium consumption in rice seedlings [53]. Wang et al. [54] elaborated that when external abscisic acid was introduced utilizing two ***Solanum photeinocarpum*** ecotypes (mining and farmland), both ecotypes showed a rise in cadmium level. Since the relation between cadmium and abscisic acid depends on plant species, the exogenous application of abscisic acid will give results other than Cd-treated ABA production (Table 1). Pompeu et al. [55] verified that the pathway by which abscisic acid interacts with the cadmium involves noticeable histological and biochemical changes. They also mentioned that ABA in tomatoes facilitates the stress response of cadmium (Table 1). Abscisic acid regulates cadmium-precipitated activation of the cysteine biosynthesis enzyme O-acetylserine (thiol) lyase (OASTL) [48].

BjCdR55 (RNA binding protein) and BjCdR39 (aldehyde dehydrogenase) expression was observed in abscisic acid signalling [56]. Their expression in ***B. juncea***, triggered by cadmium, assisted the participation of the abscisic acid signal transduction element in the existing cross-speech among the water stress-genrated and cadmium-induced signalling. It was observed that aquaporins PIP1 and PIP2 transcribed in ***Brassica juncea*** when subjected to cadmium for 12-24 hours along with BjCdR39 and BjCdR55 expression. The above observation suggested that Cd induces water stress and Cd and ABA are synergistic. BjCdR15 is the ***Arabidopsis*** TGA3 reported ortholog. TGA TFs are in the bZIP transcription factors group that is found in every eukaryotic organism. Particularly, TGA factors attach to TGACGTCA. BjCdR15 up-regulates in plants that are subjected to Cd for six hours [56]. Both BjCdR15 and TGA3 reacted to treatment when the plant is treated with abscisic acid. Yet, TGA3 has demonstrated more susceptibility than BjCdR15 to ABA [57].

Copper is another important heavy metal. Cu^{2+} soil pollution constantly infiltrates the food chain and is a potential hazard to human safety and a significant risk for environmental protection [58]. In small concentrations, copper is needed for normal plant nourishment and growth, but at a higher degree, it causes phytotoxicity [59]. Plants establish a robust mechanism of defense against numerous abiotic and biotic stresses involving the activity of antioxidant enzymes by plant hormones, like ABA [60], auxins [61], cytokinins [62], ethylene, brassinosteroids, salicylate, polyamines, and jasmonic acid [41].

The metallic impact of both Cu^{2+} and Cr^{6+}, eventually resulting in the release of oxidants and free radicals, may be responsible for oxidative stress in plant metabolism. The production of exogenous or endogenous abscisic acid increases whenever Cr^{6+} and Cu^{2+} stress occurs. It also explains the ABA's involvement (Table 1) in the tolerance of heavy metal stress [41]. The use of silicone is thought to improve the tolerance capability of plants against abiotic stress. Following different stress periods, silicone remarkably enhanced rice development and growth and minimized the harmful impact of copper and cadmium [63]. A decrease in metal intake has been found to result in the modulation of ABA phytohormone that is linked with the stress response.

Srivastava et al. [64] have identified three major abscisic acid associated genes, which involve abscisic acid inducible PP2C1 (HAI1), abscisic acid interactive protein 2 (AIP2), and abscisic acid insensitive 1 (ABI1) in ***Brassica juncea***. When the glutathione peroxidase (GPX) gene is subjected to Cu and As stress, it up-regulates in reaction to abscisic acid. GPX6 gene enormously up-regulates under the stress of copper in ***Arabidopsis*** [65]. GPX6 gene encodes isoforms in mitochondria and cytosol. Other studies have verified that in plants, GPX3 has multiple functions, i.e., signal transmission in guard cells and H_2O_2 homeostasis. In a study by Miao et al. [66] it has been explored that this signal controls the stomata in accordance with abscisic acid. Consequently, during As stress, the expression of GPX3 and GPX6 regulated the ROS level and stomata opening at different time durations.

6. DROUGHT STRESS

Drought, a major abiotic stress, antagonistically influences plant development, growth, and yield production [67]. More than half the Earth's area is vulnerable to drought and is composed of a large part of arable land [68]. The phytohormone abscisic acid regulates the abiotic stress mechanism of plants and imparts an important role in the plant response to stressful conditions and growth processes, such as seed dormancy [37,69-71]. Conditions of drought produce osmotic stress in plants that ultimately directs to drying and water intake resistance. Abscisic acid grows under osmotic stress and functions as a regulator (Table 1) in plant response to stress and plant tolerance [72,73]. After exogenic use of ABA or overexpression of genes, ABA is considered to have a positive effect on stress tolerance because of its enhanced endogenous level in plants. The exogenous addition of salicylic acid (SA), abscisic acid, and γ-aminobutyric acid (GABA) maintains leaf water content and membrane stability in creeping bentgrass (***Agrostis stolonifera***) causing an increase in the drought-induced damage [74]. Following an analysis of its metabolic activity, SA, GABA, and ABA were seen to influence normal metabolism and cause distinctive modifications in metabolite aggregation due to drought stress [74].

Drought stress influences the expression of key constituents of abscisic acid signalling, relative to protein phosphatases 2C (PP2Cs), abscisic acid, SnRK2 protein kinases in subclass III, and RCAR/PYL/PYR ABA receptors [75]. High salinity, cold, and drought could lead to a hyper-stimulation of the ABA metabolism in plants [15], and transport [76] by causing cellular desiccation during seed development in vegetative growth [37]. Drought-mediated stress increases the abscisic acid concentration in ***Arabidopsis*** leaves and protects the plant from symptoms of disease linked with avirulent type of ***Pseudomonas syringae*** pv. tomato [77,78]. ABA level is 40 times higher during drought and salt stress in continuously dividing tissues [79]. Transgenic plants, in comparison to mutants with inactive abscisic acid biosynthesis, are particularly less susceptible to environmental variations and can generate high hormone response and predict higher abiotic stress tolerance relative to the wild type [24,80]. There is an up-regulation of the ramie BnbZIP3 gene while high salinity, drought, and abscisic acid are found in ramie [81]. The gene BnbZIP3 is a member of the bZIP TFs group. It is known that the BnbZIP3 promoter contains numerous cis-acting components involved in abscisic acid signaling and multiple stress reactions.

SnRK2s, RCARs/PYL/PYR, bZIP, and PP2Cs TFs are identified under in vitro system, which involves the primary abscisic acid facilitated signalling mechanism [71]. In a nutshell, core abscisic acid signalling elements effectively control the abscisic acid communication mechanism to address dehydration. The relationship between drought induced osmotic stress and two cellular pathways; one being independent of ABA and the other ABA-dependent, has already been reported. Low-temperature stress stimulus persuades by means of modified gene expression by a mechanism independent of abscisic acid. The accessibility of the cis-acting component known as ABRE (abscisic acid-responsive) activates the ABA determined pathway [16]. Gene based experiments suggest that there is a co-relation among abscisic acid-independent and abscisic acid-determined channels and cross-speech or interaction of the molecules concerned with signalling pathway. Calcium serves as a peripheral stress reliever and a possible cross communicator. Extensive research has verified that the sudden increase of calcium levels in plant cells is due to abscisic acid, drought, high salinity, and cold [16,38].

7. UV RADIATION STRESS

The wavelength of 200 to 400 nm of the solar electromagnetic spectrum falls under the group of UV radiation. Ultraviolet radiation possesses a short wavelength which distinguishes it from the photosynthetically active radiation having a 400–700 nm wavelength. The UV rays include three forms of radiation, i.e., ultraviolet-A (UV-A), ultraviolet-B (UV-B), and ultraviolet-C (UV-C). The Ultraviolet-C rays are characterized as having a shorter wavelength of 200-280 nm. UV-C rays release high-energy photons that do not get to the surface of Earth as they have been taken by the ozone layer.

Plants are considered sessile living things that are linked to one place and require energy from the sun for normal development and growth, hence are subjected to UV rays that possess around 7 percent of electromagnetic radiation emanating from the sun [78]. The ozone layer captivates a major part of the UV-B rays, and the prevailing radiations are transferred to the surface of the Earth [78]. A higher proportion of UV-B radiations regulate ROS that causes bio-molecular damage and mutilates plant physiology, cell morphology, membrane integrity, and therefore influences development and growth that can be seen in various plants [45,82-84].

ABA acts as the principal stimulus to close the stomata, but it also plays a significant part in plants adapting them to UV-B emissions and drought [85]. The abscisic acid pathway involves hampering the ethylene (C_2H_4) production in plants as well as promoting plant development and growth [1]. The synthesis of ethylene in plants rises with UV-B radiations and under drought conditions (Table 1). The plant species that are exposed to ultraviolet-B radiations are known to have a high tolerance against drought, and thus ABA acts in multiple ways to respond to water-deficient conditions [7].

In a review by Kunz et al. [86] it is verified that ultraviolet-B radiation exposure in ***Arabidopsis*** generates tolerance against pathogen ***Hyaloperonospora parasitica***. Plant defensin 1.2 is a gene that participates in plant defense mechanisms. UV-B rays up-regulate this gene and its expression is restrained by ABA [87]. Ultraviolet-B radiation regulates UVBoxANAC13 (cis-regulatory factor). However, in various environmental stress conditions, this novel cis-regulatory factor is restricted [88]. In corn, leaves promote the synthesis of abscisic acid when subjected to ultraviolet-B rays [78]. In this specific condition, the level of hydrogen peroxide and nitric oxide has been increased. Moreover, abscisic acid is important to NO involved diminution of the harmful impacts induced by ultraviolet-B radiations (Table 1). Thus, it is proven that ultraviolet-B radiations affect the upsurge of ABA in corn leaves (Table 1).

Various studies attempt to link UV-B radiation and abscisic acid interactions, although some conclude that the existence of ABA enhances grapevine resistance to ultraviolet-B radiation [89,90]. Rakitin et al. [91] observed similar results in ***Arabidopsis*** leaves that had a positive UV-B impact on the synthesis of abscisic acid in tissue during high UV-B exposure. Further studies have proved that in drought conditions, interactions among water stress situations with ultraviolet-B radiations have shown reduced susceptibility to ultraviolet-B in different species of plants [30].

Earlier studies have verified that ABA protects leaves of maize when subjected to ultraviolet-B radiations. The results were seen by using the vp14 maize mutant that is ABA-synthesis inactive. VP14 gene is responsible for the transcription of an enzyme, 9-cis-epoxycarotenoid dioxygenase (NECD) [18]. The NECD breaks epoxycarotenoid that transforms into xanthoxin to produce abscisic aldehyde using a short-chain dehydrogenase/reductase (SDRI). Later, the aldehyde oxidase (AO) enzyme modifies abscisic aldehyde to form abscisic acid. The relationship between nitrogen oxide management and ABA appears to be discussed. It is known that NOS-like activity forms UV-B generated nitric oxide and ABA-induced nitric oxide [92]. In contrast, some scientific information recommends that nitrate reductase in guard cells is the primary cause of nitric oxide in response to abscisic acid induced hydrogen peroxide synthesis [93]. Very confusing text. Authors are unable to connect and discuss the information they present

8. WATER STRESS

Water shortage is an important limiting parameter in plant development since plants are regularly subjected to several water stress levels under field conditions. Water scarcity affects stomatal conductance, photosynthesis, metabolite aggregation, and transpiration [85], and leads to a substantial reduction in crop productivity and growth [94]. The phytohormone ABA plays an important role in numerous physiological plant mechanisms. Plant reactions to drought conditions include changes in morphology and biochemistry that in non-acute conditions lead to acclimatization and, in severe cases, have a negative impact on plant growth and plant components [7]. As the concentration of ABA in water-stressed vegetation is higher than that of the sufficiently watered crops, Sangtarash et al. [85] hypothesized that the effects of abscisic acid on adequately watered plants would be much increased compared to water-stressed plants (Table 1).

In the past 28 years (Why 28 years?), the elevating concentration of abscisic acid has been expected to restrict plant growth, especially inhibiting shoot growth in a drought resistant plant [95]. Numerous studies exhibiting the interaction between abscisic acid of plant tissue and growth inhibition indicated that a higher degree of endogenous abscisic acid was adequate to sustain growth in drought tolerant plant and growth inhibition was not fully induced by water stress [85].

Several research has demonstrated that in various plant species during the embryogenesis of seeds, the particular mRNA and proteins are assembled late due to the ABA content [96]. In water-stressed plants, drought, sodium chloride, and high osmoticum are the factors responsible for increased abscisic acid levels in plant tissues [7]. It results in the accumulation of nucleic acid and proteins, which leads to intra-cellular osmolarity and helps in different defensive functions.

Abscisic acid was also observed inhibiting the growth of the shoot in sufficiently watered plants (Table 1). However, numerous studies have shown that in drought conditions, abscisic acid insufficiency in plants increases shoot growth. Similarly, it is expected that the accumulation of endogenous ABA causes inhibition of plant growth. In maize seedlings with ABA deficiency, the shoot elongation was reported to be high compared to control [97]. In water stress conditions, ABA may restrain ethylene production from plant tissues [33]. Consequently, abscisic acid accumulation during drought conditions could retain shoot growth and root development, rather than avoiding growth that is probably believed (Table 1).

It is assumed that abscisic acid controls the equilibrium between environmental reactions and inherent growth. AtABCG25 functions as a plasma membrane abscisic acid carrier transporting abscisic acid from cytoplasm to the external surface of cells. AtABCG25 over-expression in plants results in a reduction of transpiration without retarding growth. The plants with over-expressed AtABCG25 show a specific abscisic acid reaction in guard cells. Moreover, the plants with over-expressed AtABCG25 were found to be more drought tolerant [98].

9. ROOT GROWTH AND SEED GERMINATION ABSCISIC ACID REGULATION How does this topic relate to stress?

Abscisic acid is an important plant hormone that imparts a significant function in regulating both developmental and physiological affairs in plants such as seedling development and growth, seed dormancy and multiple abiotic stress responses [6,8,33,72,99]. Several experiments illustrate the range of genes involved in these mechanisms. The genes abi1 and abi2 restrict multiple ABA reactions involving the inhibition of seed germination and stunted plant growth while the genes abi3, abi4 and abi5 exclusively exhibit ABA insensitivity during early seedling growth and seed germination [100].

Phosphorylation is also an essential signaling mechanism. The importance of phosphorylation is defined through a thorough study of the activation of abscisic acid reaction components, i.e., ABRE binding elements known as ABREs/ABFs. ABF is a primary leucine zipper-type (bZIP) transcription factor (TF) that helps in ABA signaling. Such ABA-reactive genes encode several factors, including enzymes, identified proteins, required for osmolyte synthesis, or other TF’s necessary for controlling various modifications in gene expression [33,101].

The protein kinases regulate stomatal responses to abscisic acid which is a deviation from the usual method [102,103]. ABA activates SnRK2.8, SnRK2.7, SnRK2.6, SnRK2.3, and SnRK2.2 after expression in *Arabidopsis* protoplasts [104].

Even though the signalling of ABA is related to numerous genes, some key components remain under study. The ABA signalling process is regarded as a highly connected system. It has previously been noted that SnRK2.6 helps in the positive regulation of abscisic acid signalling; nevertheless, it is only functional in the abscisic acid response of the guard cells [100,102]. In comparison, ABI1 and ABI2 negatively control seed development, seed germination, and stomatal closure [100]. This circumstance underlines the problem of which protein kinase is involved in the positive control of abscisic acid signals for seed germination and seedling production. Furthermore, snrk2.3 and snrk2.2 plants are insensitive to abscisic acid throughout the seed germination process and are protein kinases that emphatically regulate the signalling pathway throughout the germination process. The other functions of seed dormancy, gene expression induced by ABA, pro-stocking, and seed production inhibition by ABA also concern SnRK2.2 and SnRK2.3. Numerous ABA-prompted genes exhibiting reduced abscisic acid response in snrk2.3 and snrk2.2 are believed to have ABREs in their promoter area. Through the process of phosphorylating one or more ABFs, SnRK2.3 and SnRK2.2 influence the expression of such genes and thus, the binding of ABFs to ABRE [100].

The regulation of seedling growth and seed germination determines the existence of the following generation. At the time of transformation from a dormant phase to germination and from germination to development, there are important checkpoints as well [105]. In a review, rare earth elements (REEs) were reported to have harmful biological effects on yield and plant growth [106]. However, ABA signalling did not show when these REEs were integrated into phytohormone. A review by Jianrong et al. [106] shows the relation between ABA signals and Lanthanum (La^{3+}) in the developing root of ***Arabidopsis***. The concentration of abscisic acid used also influences this mechanism, that is, the root was elongated and the seed germination rate was impeded in ***Arabidopsis*** when one μ mol/L of abscisic acid was introduced. But the impacts of ABA have been reversed after ten μ mol/L of La^{3+} is incorporated. Moreover, abscisic acid promoted root hair growth, while La^{3+} impeded root hair development. Furthermore, multiple experiments have shown that La^{3+} inhibited the H_2O_2 formation induced by abscisic acid [106]. Generally, the relation between abscisic acid and La^{3+} may exhibit a direct connection with La^{3+} controlled H_2O_2 signal in root cells.

Different genetic studies have identified various *Arabidopsis* mutants with different susceptibility to abscisic acid [107]. One of the abscisic acid insensitive mutants, *abi5*, was found to evolve under an increased concentration of abscisic acid. As previously explained, *ABI5* codes for bZIP TF which, if assembled, inhibits seedling growth and germination of seed [108]. *AtEM* genes code for the class I LEA proteins that are necessary for seed maturity [109].

10. FUTURE PROSPECTS AND CONCLUSION

The signals detected in response to several abiotic stresses can be converted by abscisic acid as it is a principal signalling compound. While genes linked to abscisic acid are known to possess biological importance in the promotion of stress tolerance, a research gap is still present in the development of crops which have considerably increased stress resistance in fields. As a consequence, certain genes which have proven successful for stress resistance under greenhouse testing must be tested in the field before they are incorporated into a breeding program. Moreover, the complex process for producing stress resistance in plants must be revealed by following much comprehensive and detailed genome studies to find the main elements of ABA-mediated developmental mechanisms and make instruments for breeding and genetic engineering of stress-resistant plants. In order to expand on the complicated characteristics of abiotic stresses, it will also be essential to recognize the functions and significance of all ABA-responsive genes. A comprehensive insight into the role of abscisic acid will be given in the future by an analysis of the effect of ABA mediated genes on stress resistance in conjunction with different stress conditions.

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