

Ethylene Signaling in Plants: Possible Crosstalk and Role in Stress Tolerance

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Abstract

Ethylene, a gaseous phytohormone, serves as a key regulator in governing diverse physiological mechanisms in plants, involving maturation, growth, and responding to environmental challenges. This review investigates the intricate signaling cascades associated with ethylene and its role in enhancing plant resilience to stress. Ethylene signaling predominantly operates through a sophisticated network involving receptors, transcription factors, and downstream effectors, collectively modulating gene expression and cellular reactions. Recent studies have unveiled extensive interplay between ethylene

and other signaling passages, such as 2 hydroxybenzoic acid, trans-jasmonic acid and absisic acid, underscoring the integrated nature of plant stress responses. The review searches into the molecular mechanisms underlying ethylene-mediated stress tolerance, elucidating its impact on various stressors like drought, salinity, and pathogen attacks. It discusses ethylene's dual function as both a stress initiator and alleviator, highlighting the context-dependent nature of its effects. Additionally, the review explores ethylene's role in adapting plant defense mechanisms, including the regulation of reactive oxygen species (ROS) and polyphenolic compounds. A comprehensive consideration of ethylene signaling and its interactions with other pathways provides valuable insights for devising approaches to boost crop immunity against stress. The review also highlights the potential applications of manipulating ethylene signaling for crop improvement under unfavorable environmental conditions, emphasizing the importance of targeted strategies to modulate ethylene responses while preserving overall plant health. In conclusion, unraveling the complexities of ethylene signaling and its crosstalk with other pathways holds great promise for advancing our understanding of plant stress responses and cultivating resilient crops for sustainable agriculture.

Keywords: Ethylene; Signaling; Abiotic stress; Cross talk

Introduction

Ethylene, the initial plant hormone found in a gaseous state is to be recognized, having an important part in controlling diverse facets of plant maturation and development. While its consequences were initially discovered by Russian physiologist Dimitry K. Neljubov in 1901, it wasn't until 1965 that ethylene was formally identified as a hormone produced by plants [1]. Pathway for ethylene production was explicated out between the 1970s and 1980s, with further insights into its components of signaling emerging in the 1990s, mitigated by utilizing the artificial organism *Arabidopsis thaliana* for genetic studies [2]. Subsequent research has a plethora of genes and transcription factors downstream of ethylene, expanding our comprehension of how this odorless and colorless hormone operates in plant physiology [3].

Due to its gaseous nature, ethylene readily diffuses to neighboring cells, primarily exerting its effects locally at the site where it's produced. Previous studies have demonstrated a significant increase in ethylene biosynthesis during processes such as ripening of fruit and ageing of leaf [4]. Ethylene is renowned to its tripartite reaction, that encompasses (i) the suppression of root or stem extension, (ii) stem protuberance (iii) an excessive curling of the apical hook [5]. Beyond its role in modulating plant development and maturation, recent analysis over last twenty years has focused on ethylene's involvement in modulating plant acknowledged to many environmental stresses [6,7].

Plants exhibit a broad arrangements of environmental factors that can induce

changes in their morphology, anatomy, physiology, biochemistry and molecular makeup [8]. It's been described that nearly half of crop losses stem from abiotic stressors like drought, flooding, heavy metals, and more. To ensure their long-term survival, plants have evolved defense mechanisms to combat these stresses. During abiotic stress, plants activate specific defense mechanisms to cope with the adverse conditions. Phytohormones and their signaling pathways play crucial roles in these responses [9]. Ethylene, one of different plant hormones, serves as both a regulator of developmental processes and stress response hormone. In the face of various stresses in the environment, plants trigger the synthesis of ethylene to initiate adaptive responses [10].

The enzymes 1-aminocyclopropane-1-carboxylic acid synthases (ACSs) and 1-aminocyclopropane-1-carboxylic acid oxidases (**ACOs**) are pivotal in the biosynthesis of ethylene in plants. ACOs, encoded by a multigene family, are responsible for catalyzing the final step of this process. In species such as *Arabidopsis thaliana* and *Solanum lycopersicum*, six genes encoding AtACO and LeACO, respectively, have been identified [11]. During various abiotic stresses, ethylene biosynthesis is tightly regulated through a feedback system involving multiple signaling molecules, such as nitric oxide (NO), hydrogen sulfide (H₂S), and others (Figure 1). For instance, in rice (*Oryza sativa*), auxins have been shown to stimulate ethylene production by modulating ACO transcription [12]. However, Zhu et al. (2006) reported that NO exerts a negative regulatory influence on ethylene biosynthesis. Ethylene plays a crucial role in facilitating the accumulation of reactive oxygen species (ROS) during various environmental stresses, including exposure to heavy metals, high salinity, drought, and low temperatures. The signaling and synthesis of ROS are primarily regulated by ethylene-responsive transcription factors, particularly members of the AP2/ERF gene family, thereby linking ROS with ethylene signaling pathways in response to diverse abiotic stresses. In *Arabidopsis thaliana*, Ethylene Overproducer 1 (ETO1) has been identified as a positive regulator under salinity stress, promoting ROS generation while maintaining Na⁺ and K⁺ ion homeostasis. Importantly, maintaining ROS balance is essential for regulating stress responses and influencing plant development under the control of ethylene.

During different phases of various stresses, the downstream signaling of ethylene often relies on reactive oxygen species. For example, in the initial phase of stress, ERF74 enhances reactive oxygen species production by modulating the appearance of genes like RbohD, which subsequently promotes the activation of scavenging different genes of ROS [13]. Research on *Arabidopsis* indicates that undergoes ozone stress, the synthesis of glutathione is upregulated compared to ethylene-insensitive (ein) plants, and this process is undergoing the regulation of ethylene [14]. The relation between ROS and Ethylene is also evident in rice under metal stress. Ethylene synthesis increases under cadmium stress caused by the aggregation of ACS6 and ACS2 transcripts [15]. Additionally, ethylene is well-

recognized for its role in flood tolerance, particularly in rice varieties adapted to slight submergence conditions [16].

It has been discovered that ethylene synthesis is augmented during re-oxygenation [17]. Detailed investigations in *Arabidopsis* disclosed that group VII ERFs play a regulatory role in responding positively to hypoxic stress and flooding [18]. Primarily, under conditions of oxygen scarcity, ethylene aids plants in acclimatizing through processes such as adventitious root formation, aerenchyma development, elongation of petioles/stems, and hyponasty responses [19]. In conditions of oxygen deficiency caused by waterlogging, ethylene biosynthesis increases, accompanied by the expression of multiple ethylene-responsive genes, including a specific group of ERF/AP2 transcription factors in *Arabidopsis thaliana*. In the *Arabidopsis* *eto1* mutant, ethylene has been implicated in the regulation of stomatal opening and closure [20]. However, contrasting findings suggest that the ethylene signaling components EIN3 and ETR1 may not be directly involved in stomatal closure movements [21]. Ethylene regulates stomatal closure during stress by suppressing (ROS) formation in guard cells through flavonol production, facilitated by an EIN2-moderated track [22]. Elevated levels of ethene have been described in various species of plants, including orange, Green bean and faba bean, orange, undergoing water stress circumstances. In Thale cress, the use of integral promoter 35 S: ERF1 results in water stress tolerance, with the ethylene responsive factor protein binding to the DRE element of the RD29B promoter [23].

Ethylene signaling and signal transduction pathway

The initial step in ethylene discrimination involves the attachment of Ethylene to its receiver. These receivers of ethylene share similarity with bacterial two-component system receptors, which signal through phosphorylation happens on a histidine residue, then the po_4^{-3} group moved to an aspartate residue within the receiver domain of a response regulator protein [24]. Receptors of ethylene, along with other two receptors such as cytokinins and phytochromes receptors, are obtained by plants from cyanobacteria, the ancestors of chloroplasts. Recent evolutionary analysis data implies a common ancestry of the ethene binding domain in plants and cyanobacteria [25]. Interestingly, ethylene binding has been detected across various cyanobacteria, and in particular, *Synechocystis*, at least one cynobacterial species, harbors a functional ethylene receptor responsible for regulating cell facet characteristics, influencing phototaxis and biofilm formation. Furthermore, the affinity of ethylene binding to certain cyanobacteria and the ethylene receptor expressed in a different host in *Synechocystis* resembles what has been noted in plants, indicating saving of this domain across those organisms. Although, the original organism where ethylene receivers first emerged persists unidentified. The presence of genes encoding for proteins with potential ethylene binding domains in other bacterial phyla complicates efforts to determine the origins of these receptors [26].

In contrast, while certain ethylene receptor isoforms in plants still possess the activity histidine kinase, its significance in ethylene perception is negligible, unlike the cyanobacterial system where phosphotransfer plays a central role in receptor function. Moreover, some plant ethylene receptor isoforms exhibit serine/threonine kinase activity, suggesting a divergence in the outputs of these receptors from their ancestral proteins. Further details on ethylene receptors in nonplant species are elaborated in recent reviews [27].

Plants possess multiple isoforms of ethylene receptors. Initial studies recognized ethylene binding sites within the endoplasmic reticulum (ER) of plants membranes. Succeeding investigations on specific receptor isoforms across various plant species confirmed their localization in the ER. In *Arabidopsis*, five isoforms have been characterized: ETR1, ERS1, ETR2, ERS2, and EIN4. Variations that disrupt ethylene binding in any of these receptors result in ethylene insensitivity in plants. Furthermore, certain mutations in these receptors do not affect ethylene binding but impair downstream signaling, also leading to ethylene insensitivity [28]. Plant receptor isoforms exhibit a conserved domain architecture. At the N-terminus, they possess three transmembrane α -helices that constitute the ethylene-binding domain. This is followed by a GAF domain (named for its presence in cGMP-specific phosphodiesterases, adenylyl cyclases, and FhlA) and a C-terminal kinase domain. Three out of the five receptors also possess a receiver domain akin to those discovered within bacterial two-component receptors. These receptors are classified into two subfamilies, with ERS1 and ETR1 belonging to subfamily 1, while the other three isoforms are in subfamily 2. At N terminus, the receptors of subfamily 2 contain additional amino acids whose function remains unknown [29].

The receptors exhibit varying kinase activities, further distinguishing them. ETR1 displays histidine kinase activity, while EIN4, ERS2, ETR2 and ERS2 exhibit serine/threonine kinase activity. ERS1 has been reported to possess both types of kinase activity depending on assay conditions, though it is believed to primarily function as a serine/threonine kinase *in vivo*.

The receptors create homodimers, stabilized at their N-termini by two disulfide bonds; however, these bonds are not essential for ethylene binding to ETR1 or for its functionality in plants. Dimerization between monomers in ETR1 likely occurs between the histidine phosphotransfer (DHp) and dimerization domains of each kinase domain [30]. While dimerization between kinase domains of other receptor isoforms transpires remains unclear. Heterodimerization is also suggested as a possibility. Evidence supporting their role as receptors includes their high-affinity binding to ethylene and the observation that specific variations in any of these proteins result in ethylene sensitivity. Similarly, proteins from tomato exhibit high-affinity ethylene binding, and mutations in them lead to ethylene insensitivity [31].

Ethylene attaches to the N-terminal transmembrane region of receptors expressed heterologously with reported K_d values in the nanomolar range, correlates the ethylene binding affinities observed in plants. One distinction

between heterologously expressed receptors and those in planta is the dissociation of ethylene, which occurs with a single, slow rate in the former, characterized by a half-time of release of approximately 10-12 hours. Conversely, in planta, ethylene dissociation involves two rate constants: an earliest, quick release within the first 30 minutes after ethylene removal, followed by a slow release with kinetics similar to those of receptors expressed heterologously. This rapid release of ethylene in plants from receptors is likely attributed to ethylene-induced breakdown of proteins of the bound receptors. The structural characterization of the cytoplasmic domains of ETR1 has been accomplished [32].

As a result of these findings, a model of the ETR1 dimer has emerged, where the dimerization of the DHp domain of one histidine kinase domain occurs with that of the other monomer. The catalytic domain in this model, is associated with the DHp domain, while the receiver and catalytic domains are visualized to project outward from the DHp pair. The orientation of the receiver domain relative to the rest of the protein is predicted to differ from prokaryotic histidine kinases, suggesting a potential functional divergence of this domain from prokaryotes. Moreover, structural investigations reveal differences in the orientation of the γ -loop of ETR1, a part of the catalytic region of receiver domains, compared to characterized prokaryotic receiver domains [33]. While no structural data describing the ethylene-binding domain have been published, a computational model exists. This model, combined with previous research, indicates that ethylene binds within helices 1 and 2, with signal transduction occurring via helix 3. However, the mechanistic details of this transduction through the receptor remain elusive. A central challenge in ethylene signaling has been understanding how proteins achieve high-affinity ethylene binding, and mutational studies have discovered amino acids in helices 1 and 2 as crucial for this binding [34].

Initially, based on olefin chemistry, various transition metals were proposed as potential cofactors for binding activity. However, it was later established that ETR1 coordinates copper ions, which serve as the cofactor for ethylene binding. The presence of Cys65 in helix 2 is essential for copper coordination, as evidenced by the *etr1-1* mutant receptor carrying a Cys65Tyr mutation, which fails to bind copper or ethylene. Mutations like this render plants insensitive to ethylene. Moreover, multiple studies have shown that the ER membrane-bound copper transporter, responsive to antagonist1 (RAN1), engages in visible interactions with some of the receptors, facilitating the transport of copper and ensuring proper biogenesis of the ethylene receptors. Due to the observation that copper is co-purified with the ETR1 dimer in a stoichiometry, it was long believed that one copper ion is present in one receptor dimer.

Current experimental findings, however, suggest that each receptor dimer comprises two copper ions, with these ions likely controlled by amino acids within helices 1 and 2 of every monomer [35]. Despite this advancement, the receptor's biochemistry remains to be elucidated. While the kinase, GAF, and receiver domains are presumed to be the output domains, the precise

mechanism of Ethylene signal transduction remains elusive. This complexity is compounded by research demonstrating that although the receptors shared roles for various features, certain receptor isoforms play specific roles for particular traits or under specific conditions, sometimes exhibiting opposing roles compared to other isoforms [36].

For example, in dark-grown *Arabidopsis* seedlings, ETR1 plays a sufficient and important role in ethylene-stimulated nutational bending of stems, while the other four receptor isoforms suppress this response. Additionally, the loss of ETR1, and to a lesser extent EIN4, during seed germination, reduces the sensitivity of plants to the plant hormone abscisic acid (ABA), whereas the loss of ETR2 enhances sensitivity to ABA. Current evidence suggests that ETR2 and ETR1 signal regardless of CTR1 to induce alterations in ABA sensitivity, although the exact pathway remains unclear. These observations indicate likely variations in the biochemical response among receptor isoforms. While few of these distinctions may stem from variations in kinase specificities, this explanation does not fully account for all observed differences. Receptors of ethylene share homology with two-component bacterial receptors. The simplest two-component bacterial system involves histidine phosphorylation followed by the transfer of the phosphoryl group to a conserved aspartate residue on the receiver domain of a response regulator protein, although more intricate dissimilarities of this process be extant [37].

Although ETR1 possess histidine kinase activity regulated by ethylene, this function isn't essential for ethylene responses. Instead, it likely fine-tunes receptor signaling towards downstream elements like EIN2 interactions. Similarly, the serine/threonine kinase activity of the receptor doesn't seem necessary for ethylene responses but might modulate signal transduction of ethylene receptors and subsequent responses. Proposed receptor dimer complexes may account for the broad spectrum of concentrations of ethylene plants can respond to, and how mutations in one receptor could influence others [38].

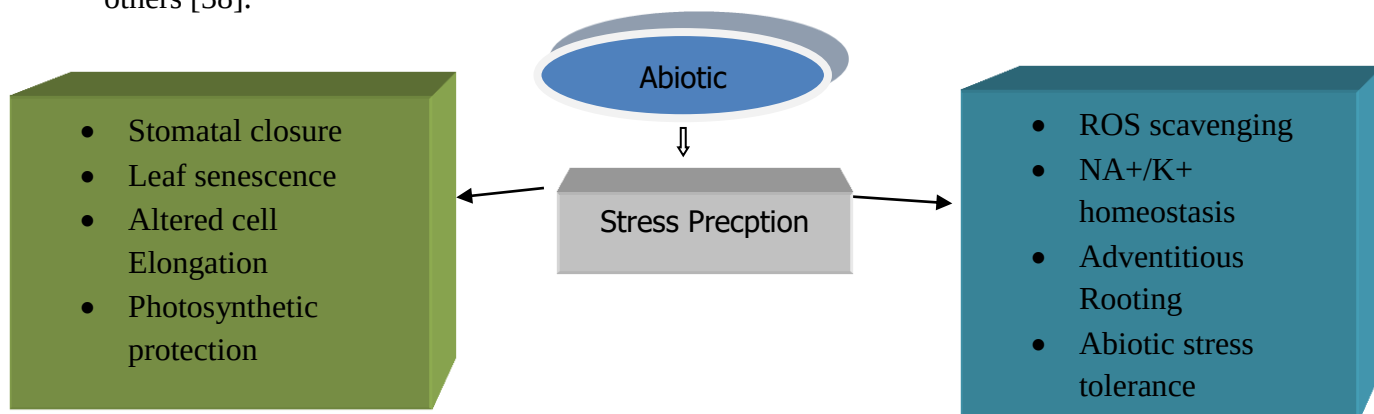


Fig1. A summary of ethylene's function in moderating the trade-off between plant growth and abiotic stress in simplified terms.

Ethylene production under abiotic stress

Constantly plants are exhibit to a diversity of environmental factors, which can lead to changes in their morphology, anatomy, physiology, biochemistry, and molecular makeup. It's been noted that around 50% of crop loss is attributed to abiotic stresses like drought, flooding, and metal toxicity [39]. To sustain these stresses, plants developed resistance processes. Among the different plant hormones, ethene serves as both a stress response hormone and a regulator of developmental processes. When plants encounter environmental stresses, synthesis of ethylene is triggered [40]. Enzymes known as ACC oxidases (ACOs) and aminocyclopropane-1-carboxylic acid synthases (ACSs) are dependable for biosynthesis of ethylene. ACOs are encoded by a gene family, with six genes reported in species like *Solanum lycopersicum* and *Arabidopsis thaliana*. Under different abiotic stresses, ethylene biosynthesis is regulated by feedback mechanisms and involves many signaling molecules like hydrogen sulfide (H₂S) and nitric oxide (NO). For instance, in rice, auxins have been found to stimulate ethylene biosynthesis by influencing the transcription of ACOs. Conversely, NO has been observed to have a negative effect on ethylene biosynthesis. Ethylene plays a key role below different environmental stresses in coordinating the augmentation of oxygen reactive entities (ROS) like metal toxicity, high salt level, low temperatures and water shortage [41]. The signaling and synthesis of reactive oxygen species (ROS) are essentially modulated by the ERF, specifically the AP2/ERF gene family, thereby linking ethylene and reactive oxygen species signaling across different abiotic stresses. In *Arabidopsis*, by increasing ROS production Ethylene Overproducer 1 (ETO1) has been identified to positively influence salt stress while maintaining Na⁺/K⁺ homeostasis. It has been highlighted that maintaining the stability of ROS is crucial for controlling plant development and stress responses mediated by ethylene [42]. Throughout different phases of stress, the downstream signaling of ethylene generally depends on ROS. For example, during the initial period of stress, ERF74 enhances ROS production by regulating the expression of genes like RbohD, subsequently promoting the expression of scavenging genes od ROS. Research conducted on *Arabidopsis thaliana* has demonstrated that during ozone stress, the synthesis of glutathione (GSH) is enhanced compared to *ein* mutants, and this process is regulated by ethylene [43]. The relationship between ethylene and ROS has also been observed in rice (*Oryza sativa*) under metal stress, where ethylene synthesis increases during cadmium exposure due to the accumulation of ACS6 and ACS2 transcripts. Ethylene is well-known for its role in flood tolerance, particularly in rice varieties that thrive under slight submergence conditions. Research has revealed that synthesis of ethylene is enhanced during re-oxygenation after flooding. Detailed studies in *Arabidopsis* have shown that group VII ERFs play a regulatory role in positively responding to hypoxic and flooding [44].

Under conditions of low oxygen, ethylene essentially aids plants in acclimating through the formation of aerenchyma, adventitious roots, elongation of petioles/stems, and the hyponastic response. When oxygen levels are reduced due to waterlogging, ethylene biosynthesis increases, and various ethylene-responsive genes, including a distinct group of ERF/AP2 genes, are expressed in Arabidopsis. In Arabidopsis, the *eto1* mutant shows that ethylene is implicated in both the closing and opening of stomatal apertures. Although, studies indicate that ethylene-responsive factors like EIN1 and ETR3 are not directly involved in stomatal closure. Instead, ethylene controls closure of stomata by suppressing reactive oxygen species formation and promoting production of flavonol in guard cells under stress conditions, utilizing the moderate pathway of EIN2 [45]. High ethylene levels have been described in different species of plants such as Green bean and faba bean, orange under drought stress conditions. Arabidopsis plants engineered with a fundamental 35 S:ERF1 exhibit water stress tolerance, where the protein ERF is directly binds of the RD29B promoter which is the element of DRE [46].

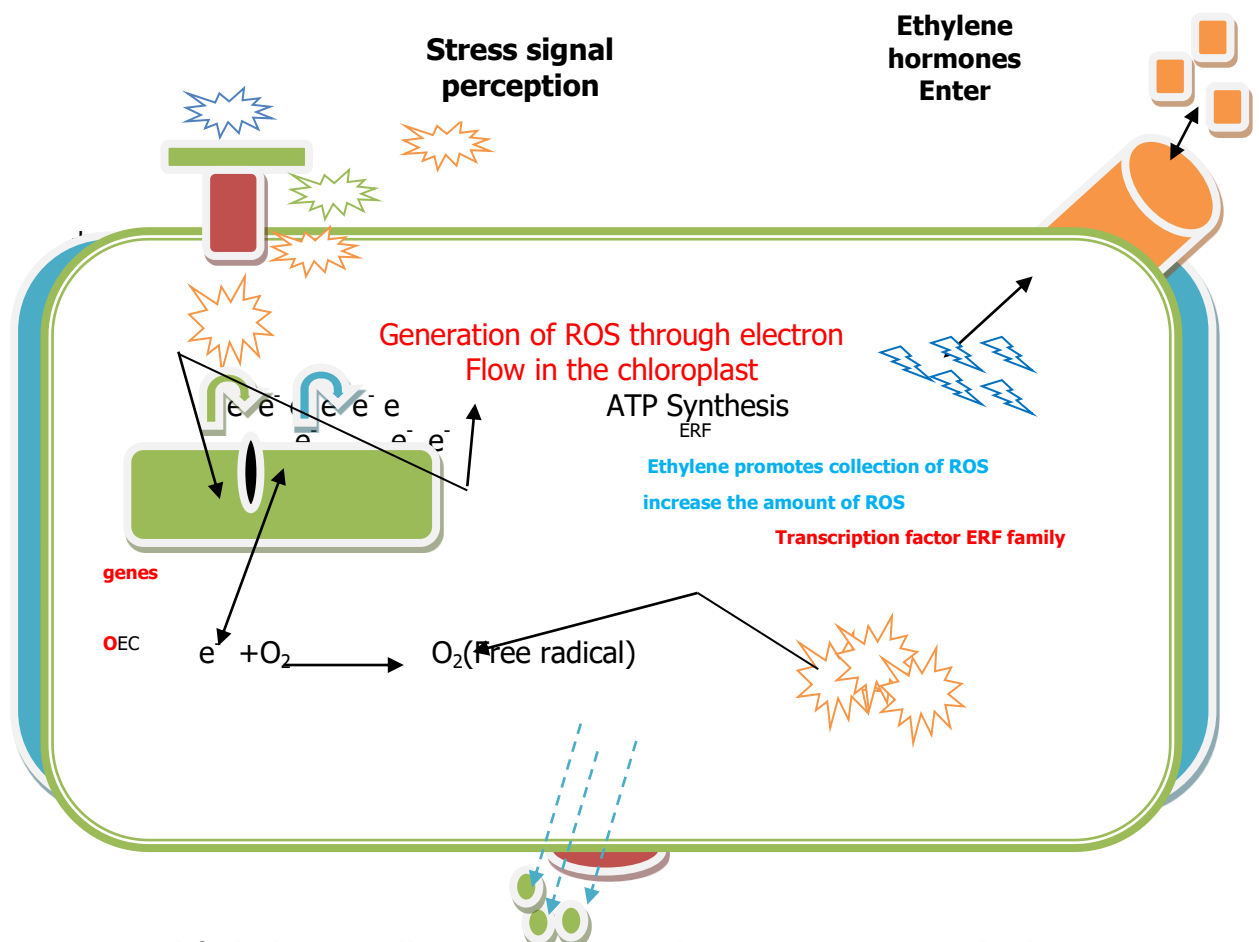


Fig.2. A simplified diagram illustrating the signaling components involved in the abiotic stress-induced downregulation of the antioxidant defense system.

Ethylene and regulation of metal stress

In addition to conventional abiotic stresses encountered in agricultural settings, such as water shortage, flooding, and extreme temperatures, heavy metal (HM) stress has emerged as a significant and widespread warning [47]. This is primarily attributed to the unregulated industrialization and urbanization witnessed over the recent decades, leading to an accumulation of heavy metals in soil. While plants naturally require more than 15 different types of HMs as nutrients for various cellular activities, excessive presence of both essential and non-essential HMs can pose challenges. Under HM stress conditions, plants frequently undergo oxidative stress as a result of immoderate ROS production and methylglyoxal [48].

Elevated concentrations of these compounds have demonstrated adverse effects on the maintenance of cell composition, inducing lipid peroxidation in membranes, deteriorating biological macromolecules, promoting leakage of ion, and causing cleavage of DNA strand, among other biochemical and physiological processes. Consequently, plant growth is hindered, leading to reduced economic yield. Furthermore, the augmentation of metal surplus in the primary food chain has been linked to significant environmental and health issues [49].

Plants employ various mechanisms to purify unwanted heavy metals (HMs). One common response to HM stress includes an increase in production of ethylenes, driven by the increased expression of genes associated with ethylene production and/or alterations in the expression of ethylene-responsive genes [50]. Traditionally, ethylene has been acknowledged for its function in regulating key plant physiological activities like root hair, seed germination, and nodule development, and maturation. However, while Ethylene has been proposed as a stress-responsive hormone that reacts to many abiotic and biotic cues, the precise function of elevated ethylene levels in response to HM stress remains unclear [51]. Studies have demonstrated enhanced production of ethylene in plants when exhibit to toxic levels of metals such as nickel (Ni), copper (Cu), zinc (Zn), iron (Fe) and cadmium (Cd). For instance, both Cd and Cu have been shown to stimulate ethylene synthesis by increasing the activity of ACC synthase, an enzyme involved in the ethylene synthesis pathway [52].

Ethylene and regulation of flood stress

The process of ethylene biosynthesis varies significantly under stress conditions compared to standard conditions. Abiotic stresses like water shortage, chilling, heat, flooding, heavy metals, and photo-oxidative stress induce ethylene biosynthesis, leading to a quick increase in ethylene levels [53]. In particular, total immersion expedites the accumulation and production of ethylene in majority of plant species [54]. Unlike other stresses where gas diffusion remains unimpaired, flooding severely restricts exchange of gases between the plant and its surroundings. Immersion triggers the ethylene biosynthesis, which becomes trapped in tissues of plants, quickly

reaching levels that saturate the response within 1-2 hours [55].

Initiating responses adapted to flooding enables a variety of species to temporarily reside and thrive in submerged environments. Comprehension the dynamics of ethylene—its perception, signaling and biosynthesis—in plants resistant to flood could prove valuable for improving the resilience of vital agricultural crops. One of flood-tolerant species, *Oryza sativa* stands out as the most extensively observed agricultural crop due to its economical and agricultural significance. In this review, we analyzed the contribution of ethene production and signaling genes in rice's reactions to submergence by examining gene expression patterns by using bioinformatics methods. Initially, genes of rice related to ethylene were identified from databases such as Rap-db (<http://rapdb.dna.affrc.go.jp/>) and Uniprot (www.uniprot.org/). A sum of 395 genes were acquired (see Supplementary Table S1) and subsequently categorized into groups comprising Ethylene biosynthesis, sensing, signaling and induced response genes (see Supplementary Tables S2, S3, S4, and S5, respectively).

Initially, in silico analysis of libraries related to submergence stress was carried out using the Rice Oligonucleotide Array Database (ROAD) (www.ricearray.org/). Subsequently, a microarray investigation was performed on aboveground tissues of both of the submergence-tolerant M202-Sub1 and the intolerant M202 rice varieties [56]. Rice accessions lacking the SUB1 gene SUB1A (such as M202) typically perish under 7 days of being fully submerged. In disparity, genotypes the contain SUB1A (e.g., M202-Sub1) can withstand submersion pressure for a period exceeding fourteen days [57]. To understand expression patterns of ethylene-related genes induced by immersions in these diverse genotypes, publically accessible microarray data from the Affymetrix Rice Genome Array were analyzed utilizing Genevestigator. The study evaluated transcriptional control in seedling submerged for 24 hours (S) in comparison to non-submersed shoots (UT), which served as the control [58].

Hierarchical clustering of fold change values by gene expression revealed that under flooding stress, the regulation of the biosynthetic pathway is similar in both intolerant and tolerant successions. Specifically, the expression of the 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) genes ACO8 and ACO3 were significantly increased in imersed shoots, while ACO1 was downregulated. Although, when comparing the intolerant (M202) and tolerant (M202-Sub1) acquistions, it was found that ethylene development was notably excessive in the submersion-intolerant genotypes as contrast to the tolerant one [59]. This differential regulation in tolerant genotype is mediated transcriptionally by the repression of the ACS gene ACS2 [60]. In paddy subjected to low oxygen levels, two ACS genes, ACS1 and ACS5, exhibit high expression levels and differential expression in different tissues under immersions. ACS1 transcripts are predominately constrain in internodes, particularly in the zone of cell prolongation, and are influenced after six hours of submersion [61].

ACS5 transcript expression occurs in areas known for extensive elongation

and cell division, such as the vascular bundles found in young stems and leaf sheaths. Changes in organ and cell shapes enable improved gases exchanges during periods of submergence stress. Elevated levels of ethylene in submerged tissues stimulate various adaptation responses, including the formation of adventitious roots, elongation of shoots, utilization of carbohydrates, development of aerenchyma, and initiation of ethanolic fermentation [62]. Specifically, while submerged, the expression of ACS1 messenger RNA enlarged solely in internodes, that harbor the zone of cell elongation, while other sections of the identicle stem, encompassing the zone of cell distinction, nodes and intercalary meristem, exhibit lower levels of ACS1 messenger RNA compared to aerial conditions. Similarly, there is an increased expression of ACS5 mRNA within the xylem and phloem found in leaf sheaths and young stems, where cells undergo robust cell elongation and division in response to stress. The findings suggest that ACS5 and ACS1 collaboratively contribute to the synthesis of ethylene under prolonged immersion, promoting the elongation of internode and active division of cell and elongation within the xylem and phloem of young stems [63].

The final enzyme in the biosynthesis pathway of ethylene is ACO, which exhibits decreased activity under limited oxygen availability. This decline occurs because ACO relies on oxygen to convert 1-aminocyclopropane-1-carboxylic acid (ACC) into ethylene. In rice plants experiencing oxygen limitation, transcripts of ACO1 gather in the elongation zones of both internodes and nodes. The induction of ACO1 occurs as early as 4 hours after submergence and persists for 24 hours. Recent research indicates that OsACO5 is prominently expressed in rice under normal conditions of oxygen, providing its central role in the emergence of aerenchyma in the oxygenated roots of rice plants. While the expression of ACO1 facilitates ethylene accumulation following the onset of aerenchyma formation, ACO5 is essential for sustaining the synthesis of ethylene in the roots [64].

The notable downregulation of OsACO1 (by more than 5-fold) observed in the tolerant M2O2-Sub1 variety may be linked to the immersions reactions governed by ethylene, like the prolongation of shoots and the suppression of the utilization of carbohydrate. Although pathways for ethylene signaling in rice remain incompletely understood, several key components have been identified. Among these are the ethylene receptors (ETRs), including OsERS1, OsERS2, OsETR2, OsETR3, and OsETR4. During submergence, OsETR2 exhibits high expression levels in internodes and is also encouraged by ethylene. Studies have shown that overexpression of OsETR2 reduces the concentrations of ethylene, while knockout plants lacking OsETR2 display heightened ethylene sensitivity. However, the precise role of these receptors in ethylene signaling within rice remains unclear. Additionally, other components involved in the ethylene signaling cascade, like OsEIN2 and OsEIN3/EIN3-like (OsEILs), have been identified as ethylene insensitive. Upon submergence, transcription factors like EIN3/EIL1 in rice are quickly encouraged by ethylene at the protein level and are crucial for organizing downstream signaling pathways of ethylene before harmful outcomes, like

lack of oxygen occur [65].

Recent findings indicate that early activation of ethylene signaling, occurring within 1 hour, involves the rapid balance of EIN3, serving as a swiftly perceived signal of flooding that saturates and promptly initiates response mechanisms. EIN3 plays a direct role in regulating downstream transcription factors crucial for various submergence-induced processes, such as underwater hypocotyl elongation in *Arabidopsis* root tips and adaptive remodeling of lipid metabolism to enhance hypoxia tolerance. Computational analysis suggests that submergence triggers ethylene signaling by modestly reducing the expression of CTR1 while increasing the expression of EIN3-like genes, induced as OsEIL1-4. Previous research by Mao et al. (2006) has demonstrated the involvement of OsEIL1 in the ethylene signal transduction pathway, where it positively regulates ethylene responses in rice. Conversely, although a slight increase in expression in the tolerant variety, OsEIL3 has been described to have a lesser impact on response of ethylene in etiolated seedlings [67].

The group of genes depicted in Fig. 2D correspond to the B-2 subgroup of ERFs (ethylene-responsive element binding proteins)/AP2 (apetala 2-like proteins), which are transcription factors (TFs) playing critical roles in processes of signaling and responses to abiotic stress, particularly in mechanisms related to submergence tolerance in rice. Based on preliminary data from rice microarray experiments, several rice group VII ERFs, including OsERF7, OsERF61, OsERF65, OsERF66, OsERF62, OsERF68, OsERF69, OsERF91, OsERF67, and OsERF96, were induced by over tenfold in response to immersions in both rice varieties. Additionally, OsEREBP96, OsEREBP89, and OsEREBP129 genes exhibited strong upregulation under submergence conditions. OsEREBP-89 has been demonstrated to be stimulated by ethylene 2,4-D, and NaCl in rice roots, with its expression further encouraged in OsEIL1-upregulating plants. Moreover, OsEREBP129 and OsEREBP96 are classified as RAV transcription factors (TFs), characterized by two domains, AP2 and B3, and are involved in developmental processes such as brassinosteroid responses [68], flowering time regulation, and leaf senescence. Although some RAV TFs have been involved in plant responses to abiotic stress such as salinity, cold and drought, their direct participation in submergence tolerance in paddy has not been established despite their significant induction (over 15-fold) under submergence in both rice varieties [69]. Consequently, targeting the modulation of biosynthesis of ethylene under submerged conditions could present promising avenues for developing immerse-tolerant rice cultivars in the future [70].

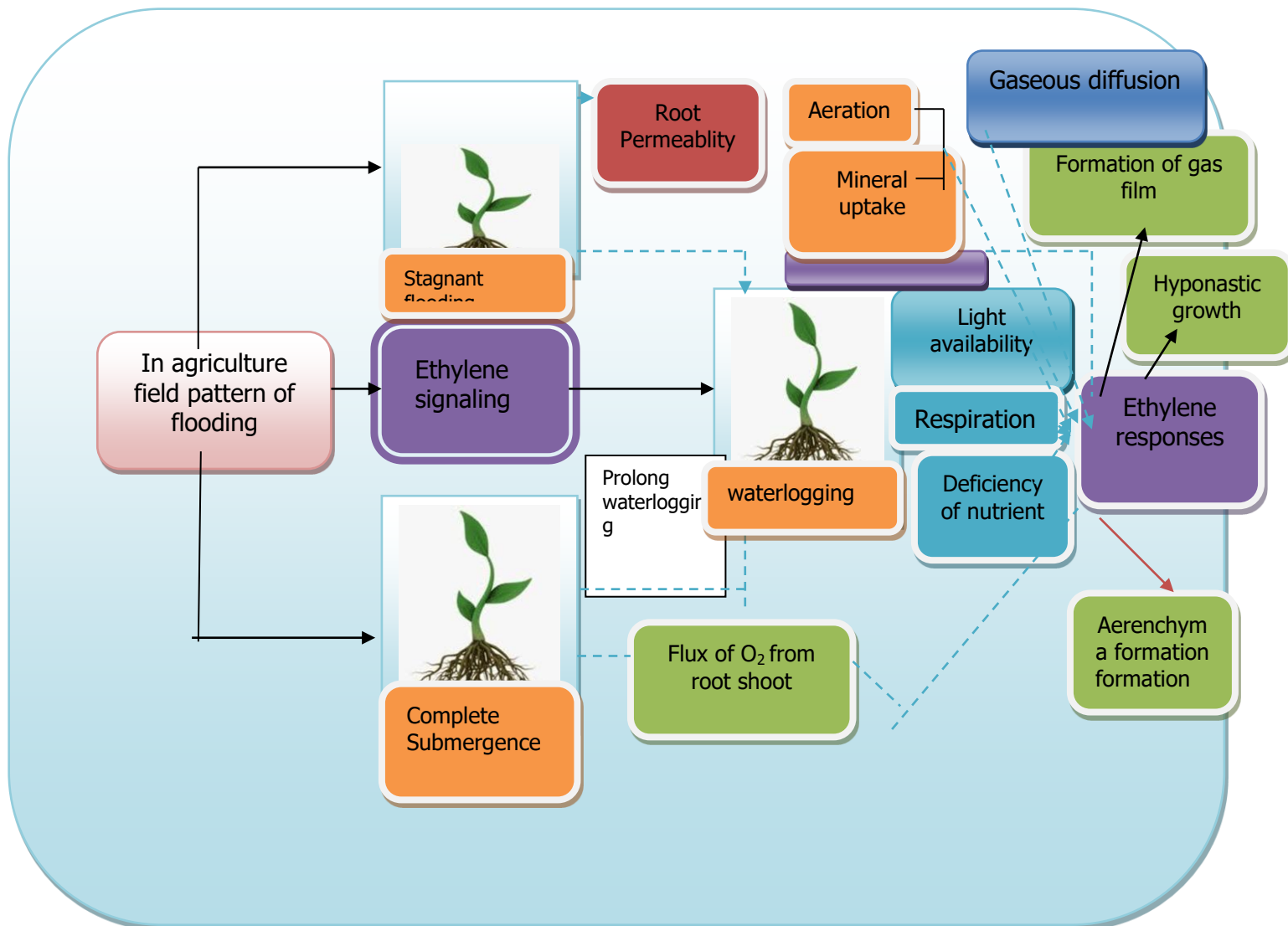


Fig. 3. Different types of flooding, its effects on plants and adaptive processes.

Ethylene and regulation of drought stress

The *eto1* mutant in the *Arabidopsis*, ethylene plays a double role in both the opening and closing of stomatal apertures. There's evidence suggesting that ethylene has a negative effect on the abscisic acid induced closure of stomata. During drought stress, wild-type plants exhibit a rapid closing movement compared to the ethylene-insensitive *eto1* mutant. Notably, factors involved in ethylene signaling, such as ETR1 and EIN3, do not directly contribute to closure of stomata. Instead, increased formation of ROS in guard cells,

facilitated by NADPH oxidase, promotes stomatal closure. Ethylene regulates the closure of stomata by obstruct the formation of oxygen reactive entities through the production of flavanols in guard cells under stress conditions, utilizing an EIN2-dependent pathway [71].

In rice, mutants of the ETHYLENE OVERPRODUCER 1-LIKE (OsETOL1) protein, such as *eto1* mutants, exhibit insensitivity to ethylene and high levels of ethylene production, aiding survival of plant under water deficit conditions. Conversely, paddy plants upregulating OsETOL1 show reduced ethylene levels, providing them less adapted to drought stress. During drought stress, various species of plants including *Vicia faba*, orange, and French bean, exhibit increased ethylene levels. The important enzyme in biosynthesis of ethylene ACS, possesses different sites of phosphorylation on its C-terminal portion, leading to three distinct types. Type I ACSs have phosphorylation zones for mitogen-activated protein kinase 3/6 (AtMPK-6) and calcium-dependent protein kinase (AtCDPK2, CDPK, or CPK). Type II ACSs contain only CPK phosphorylation zones, while type III ACSs lack any zones of phosphorylation. In maize, ethylene serves as an inhibitor leaf growth, and under water deficit conditions, ACC acts as a signaling molecule [72]. Under conditions of low water availability, the expression of RD29A and RD29B genes is upregulated. Specifically, during osmotic stress, the RD29A promoter contains two cis-acting elements: one responsive to dehydration (DRE) and the other responsive to abscisic acid (ABA), which activates the gene. RD29B, on the other hand, possesses only the ABRE domain and is activated exclusively by ABA. Arabidopsis plants engineered with a fundamentals 35S booster driving the expression of ERF1 exhibit drought tolerance. ERF proteins directly bind to the DRE element within the RD29B promoter. The series 23A/GCCGAC represents the core sequence of the DRE element, that is crucial component of the cis-acting promoter element involved in regulating gene expression during drought stress, promoting high survival rates but potentially reducing yield.

Ethylene and regulation of hypoxia and anoxia

In oxygen-deprived conditions, ethylene essentially adapts plant acclimatization by promoting the emergence of adventitious roots, formation of aerenchyma, increased height of petiole/stem, and hyponastic responses. Two transcription factors in Arabidopsis—HYPOXIA RESPONSIVE ERS1 and RELATED TO AP2.2—are in charge of different downstream signaling pathways that are affected by ethylene. In paddy fields, ethylene plays a crucial role in modulating ERF-like genes, such as SUBMERGENCE1-A-1 (SUB1A-1) and SNOKE1 (SK1) and SK2, in submerged rice plants, thereby conferring tolerance to prolonged submergence [73]. Ethylene is recognized as a crucial regulator in maintaining the balance of hormone expression, managing ROS and adapting metabolic processes during re oxygenation [74]. Despite the molecular evidence linking ethylene to hypoxia, the exact signaling pathway remains elusive. In conditions of oxygen deficiency, such as waterlogging, ethylene production increases,

accompanied by the expression of various genes responsive to ethylene includes a certain group of ERF/AP2 genes, in Arabidopsis. To enhance rice survival in hypoxic conditions, the upregulation of RAP2.2, a member of the VII AP2/ERF transcription factor family associated with SUBIA, promotes plant resilience by enhancing metabolic rates under hypoxia [74].

Ethylene and ABA interaction under abiotic stress

Like ABA, ethylene is recognized as a fundamental plant stress hormone, with interactions—both negative and positive—occurring between them depending on the developmental context. ABA influences ethylene synthesis by modulating the expression of important biosynthetic genes of ethylene, involving Acyl-CoA synthetase and ethylene response factor 11, NCED. DREB is a member of the ethylene-responsive family whose transcription is controlled by ABA at the molecular level and is activated by ethylene. [75]. Throughout different physiological processes like photoperiodic induction, leaf senescence, and fruit ripening, ABA promotes ethylene formation. Conversely, ABA inhibits ethylene formation through ABI4-mediated reduction in the transcriptional levels of biosynthetic genes of ethylene, ACO or ACS. Tosetti et al. (2021) observed that ethylene induces ABA 8'-hydroxylase activity in onion bulbs, leading to increased ABA degradation and accumulation of phaseic acid. Wang et al. (2019a) demonstrated that ethylene suppresses the transcription of ABA biosynthetic genes (NCED2 and NCED3) under ripening of fruit in *Prunus persica* using electrophoretic mobility shift and yeast one-hybrid assays. Novikova et al. (2020) described a positive relation between ABA signaling and ethylene pathways in coupling cell cleavage and differences during tissue culture. Studies in proteomics and genomics exposed that abscisic acid and ethylene crosstalk involves a common set of responsive proteins and genes, enhancing glutathione content during abiotic stress. Sun et al. (2020) described a triple interaction among ethylene, gibberellin and ABA, where ethylene primarily modulates ABA sensitivity by regulating the expression of ABA signaling genes (TaABI3) and ABA-metabolizing genes (TaNCED2 and TACYP707A1). Gibberellin sensitivity is controlled by ABA/GA ratio modulation through changes in the expression of gibberellin-metabolizing genes (TaGA20ox1, TaGA3ox2, and TaGA2ox6) and its signaling gene (TaGAMYB). Under stress conditions, ethylene upregulates EIN3 expression, repressing ABI4 levels, leading to increased expression of VITAMIN C DEFECTIVE 2 and higher ascorbic acid formation, serving as a potent antioxidant by scavenging ROS. Furthermore, a positive interaction between ethylene and ABA during flower senescence was observed, where both hormones hasten the senescence of potted flowering plants and cut flowers [76]. Chang et al. (2014) found that the application of exogenous ABA and ethylene increased PhHDZip transcript levels, consequently accelerating flower senescence in petunias. Ethylene also functions as a flowering inhibitor in short-day plants when applied during the latter half of the inductive light period. Wilmowicz et al. (2014) observed that applying

exogenous ABA just before the onset of a 16-hour long dark period inhibited flowering, an effect partly altered in the presence of amino vinylglycine, suggesting that ABA directly influences ethylene formation, thereby inhibiting flowering. Riboni et al. (2013) described that ABA-deficient mutants (aba2-1 and aba1-6) exhibited a late-flowering phenotype, directly correlated with elevated levels of the floral-suppressing hormone ethylene in the ABA mutant plants.

Table 1. Effects of various abiotic stressors on Arabidopsis signaling and ethylene biosynthesis gene transcript abundance.

Stress types	Regulation	Ethylene Biosynthetic Genes	Ethylene Signaling Genes
Heavy metal stress	Up	ACS2, 5, 6, ACO1, 2	EIN2
	Down		
Cold stress	UP	ACS2, 11, ACO2	EIN3
	Down		ETR1, EIN4, EIN2, EBF1/2
Heat stress	Up	ACS6, 7, 8, 10, 11, 12, ACO2, 4	ERS2, ETR2, EIN3
	Down	ACS2, 4, 5, ACO1, 3	ERS1, CTR1, EIN2
Salt stress	Up	ACS2, 6, 7, 11, ACO2, 4	EIN3
	Down		ETR1, EIN2
Osmotic stress	Up	ACS7, ACO2	ETR2, ERS1, CTR1, EIN3/EIL1, EBF1/2
	Down		ETR1, EIN2
Flooding /hypoxia	Up	ACS2, 6, 7, 9, 11	EIN3
	Down		

Conclusions

Ethylene plays a pivotal role in aiding plant adaptation to abiotic stress, emphasizing the need to unravel its intricate molecular interplay with both antagonistic and synergistic signaling cues. While the molecular interaction between ethylene and hypoxia is recognized, understanding ethylene signaling amidst stress remains nascent. Hence, there's a demand for precise methodologies facilitating the rapid detection of ethylene-modified proteins, vital for comprehending its function. Furthermore, exploring how ethylene emission influences neighboring flora is crucial. This knowledge can empower crops to withstand harsh environmental conditions, particularly in flood- and drought-prone regions, thereby enabling farmers to cultivate high-quality crops to sustain the population.

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