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Ethylene regulatory mechanisms and signaling towards the senescence associated incidences: A review

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Abstract: Unlike other phytohormones, ethylene is considered as an important plant gases hormone in regulating numerous plant developmental processes such as germination of seeds, elongation of cell organs, flower opening, ripening of fruit, organ senescence and as well as abscission. It holds a simple structure compared to the rest of the plant growth substances. Ethylene is normally generated by higher plants and is usually linked to fruit ripening and specific triple response. Generally, all kinds of biotic and abiotic stresses including temperature fluctuations, water imbalance, salt issues, pathogen or insect attacks holds certain specific kind of negative influence on the plants growth and development. Transcription factors are known for their crucial functions in signal transduction to trigger or repress expression of defense gene, along with in the modulation of connectivity among various signaling pathways. ERF genes are observed to be stimulated not only with disease-concerned and pathogen infection stimuli, but its expression levels can also be trigger due to abiotic stresses, thus in this way ERF genes can improve the multiple stress resistances in the transgenic plants. Furthermore, over-expression study analysis of ERF gene revealed that these transcription factors can bring a broad-spectrum resistance towards pathogens and other abiotic stresses and can also the tolerance in transgenic plants towards drought, salt, and freezing. Thus, ERF gene is focus under this specific research study in order to explore its role in relation to abiotic stress such as ethylene stimuli.
Keywords: Ethylene, biotic stress, abiotic stress, senescence, abscission, transcription

INTRODUCTION

Several studies have been demonstrated that ethylene characteristically involved in a broad range of developmental processes and physiological responses such as flowering, fruit ripening, organ senescence, abscission, nodulation of root, seed germination, programmed cell death, cell expansion, and responses to abiotic stresses [1]. Besides, in context to this regards various studies have been demonstrated that ethylene characteristically functioned in plant growth and development as a key modulator of cell expansion and also promote the cell division [2, 3]. Further, reported work has also been showed that ERF proteins play important roles in the response to environmental stresses such as high salinity, drought and low temperature conditions via regulation of stress responsive genes [4-6].

Beside, its importance in many commercial industries, more predominantly recognized as one of the most crucial natural plant hormone involved in a number of important biological and physiological phenomena's of plants life. Like other plant hormones, ethylene also plays an indispensable role in most of the agricultural crops and plants and also more importantly in the post-harvest life of agriculture commodities including fruit, vegetable and flowers. All these crucial roles in the plant's physiology and biology has given an extra edge to ethylene over the other plant hormones and the multidiscipline research work exploring on the regulation and functioning basis of ethylene in various biological mechanism during plant's life has always been on priority list of scientist around the world [7,8].

Moreover, Sl-ERF.B.3 is an abiotic stress responsive gene, which is induced by cold, heat, and flooding, but down regulated by salinity and drought. To get more insight into the role of Sl-ERF.B.3 in plant response to separate salinity and cold, a comparative study between wild type and two Sl-ERF.B.3 antisense transgenic tomato lines was achieved. Furthermore, the cold stress essay clearly revealed that introducing antisense Sl-ERF.B.3 in transgenic tomato plants reduces their cell injury and enhances their tolerance against 14 day of cold stress. All these results suggested that Sl-ERF.B.3 gene is involved in plant response to

abiotic stresses and may play a role in the layout of stress symptoms under cold stress and in growth regulation under salinity [9]. Thus, the aim of present study has been planned to understand the molecular mechanism underlying the specificity of ethylene responses during plant development and growth.

Prototype of ethylene in plant growth and development

Ethylene is considered to be one of the most of crucial and important plant hormone, which are indispensably engaged in the complex physiology and biology of plant mechanism. Moreover, ethylene is essentially engaged in the structural and physical development of plant, fact about this key plant hormone is that ethylene is immensely involved in the biological adoptive mechanisms and approaches that plants acquire while confronting any kind of stressful situation such as drought, osmotic stress, and other biotic and a biotic stress [10].

Ethylene signal transduction pathway and biosynthesis

In ethylene signal transduction pathway, ERFs are considered as preceding known downstream components which are responsible for modulating the transcription of early ethylene regulated genes in plants. Being determined by one of the largest family of plant transcription factors, ERF proteins are the most suited step of ethylene signaling where the diversity and specificity of ethylene responses may originate. ERFs are part of AP2 (APETALA2)/ERF super family which also contains AP2 and RAV family genes [11]. The AP2/ERF super family is characterized by the presence of the AP2/ERF domain [12, 13], which consists of about 59-60 amino acids and is involved in DNA binding. ERF family proteins contain only one AP2/ERF domain, whereas, AP2 family genes have two such domains. RAV family proteins contain an additional B3 DNA binding domain along with AP2/ERF domain [14]. The ERF domain was first identified as a conserved motif in four DNA-binding proteins from tobacco (Nicotianatabacum), namely, EREBP1, 2, 3, and 4 (currently renamed ERF1, 2, 3, and 4), and was shown to specifically bind to a GCC box, which is a DNA sequence involved in the ethylene-responsive transcription of genes [15].

Although, in concerning with rose it has been reported that ethylene may accelerate the flower opening process compared to inhibit the expansion of petal cells. Although even to date, regulatory mechanism of ethylene response that happens during cell expansion remains uncertain. Thus numerous reports have been concluded that ethylene regulates the expression of genes associated with cell expansion, such as cell wall with ethylene exhibit a triple response, which consists of radial swelling of the hypocotyl, exaggeration of the apical hook, and inhibition of hypocotyl and root elongation.

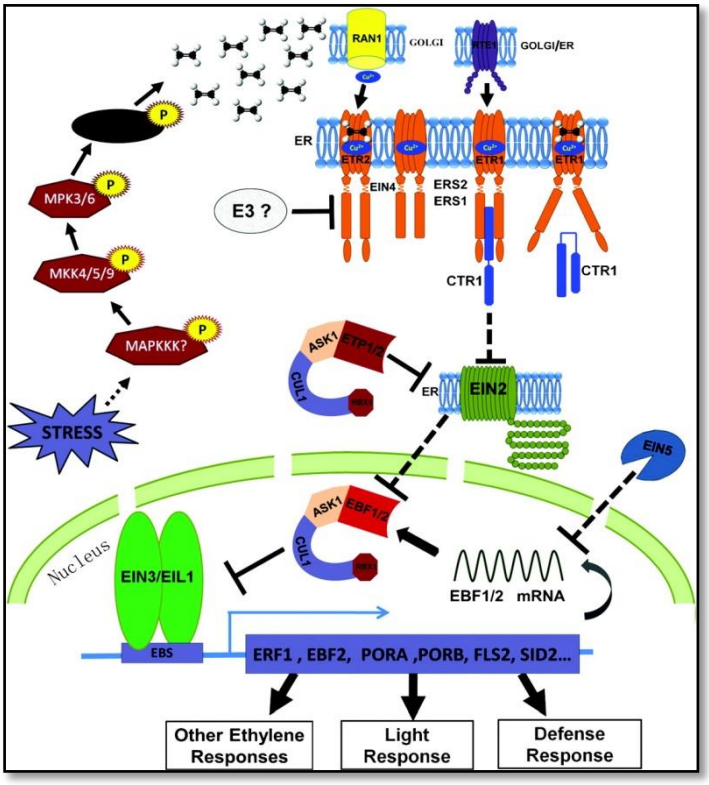

Fig 1. Biosynthetic Pathway and Regulation of Ethylene (Ohme Takagi and Shinshi, 1995)

Transcription factors which belong to the APETALA2/Ethylene Responsive Factor (AP2/ERF) family are unadventurously extensive in plant kingdom. These regulatory proteins are concerned as in the control of primary and secondary metabolism, growth and development and as well as responses to environmental incentive. Due to their flexibility and the specificity of individual members of this family, the AP2/ERF transcription factors signified as important intention for genetic engineering and breeding of crops [16]. Whereas, [17] reported that ethylene responsive element binding factors (ERF) proteins are plant specific transcription factors, many of which have been linked to stress responses. However, present work identified four Arabidopsis ERF genes whose expression was specifically induced by a virulent and virulent strains of the bacterial pathogen Pseudomonas syringae PV of tomato. The induction of ERF gene expression in most cases preceded the mRNA accumulation of a basic chitinase gene, a potential downstream target for one or more of these ERFs. Whereas, the author further revealed that the expression of the ERF genes examined among different Arabidopsis tissues, in response to the signaling molecules ethylene, methyl jasmonate and salicylic acid (SA).

Ethylene biosynthesis pathway

Basic concept in ethylene biosynthesis has been a focus of biological research study over the years in the field of phytohormones physiology [18]. Establishment and recognition of *S* – adenosylmethionine(*S*-AdoMet)and ACC as major precursors of ethylene were the main breakthroughs in ethylene biosynthesis pathway (Figure 1) [19]. Capitalizing on this learned knowledge, various biochemistry approaches were utilized to characterize and purify the enzymes that catalyze these chemical reactions. ACC synthase (ACS) and ACCoxidase (ACO) [20, 21] genes were demonstrated as the prime enzymes taking part in synthesis of ethylene. These two key enzymes belongto a multigene family which is controlled by a complex system of developmental & environmental signals that are known to responsive to various kinds of internal and external stimuli [22]. Cellular methionine besides being an integral building unit for protein synthesis, it is playing its role in sysnthesis of *S*AdoMet as nearly 80% of methionine converts to *S*AdoMet using an enzyme called as *S*AdoMetsynthetase (SAM synthetase, EC 2.5.1.6) at cost of ATP utilization [23]. Many biochemical pathways *such as* polyamines and ethylene biosynthesis use*S*AdoMet as a substrate because it's the key methyl donor in plants. Furthermore, *S*AdoMet is engaged in methylation chemical reactions which can alter proteins, nucleic acids and lipids. According to the Yang cycle, the first convincing stride in ethylene biosynthesis is the transformation of *S*AdoMet to ACC using enzyme ACC synthase (*S*adenosyl- L -methionine methylthioadenosine-lyase, EC4.4.14) [24]. Moreover, ACC synthase (ACS) can additionally generate 5'-methylthioadenosine (MTA) during this chemical reaction, which can be subsequently transformed to methionine utilizing a modified methionine cycle.

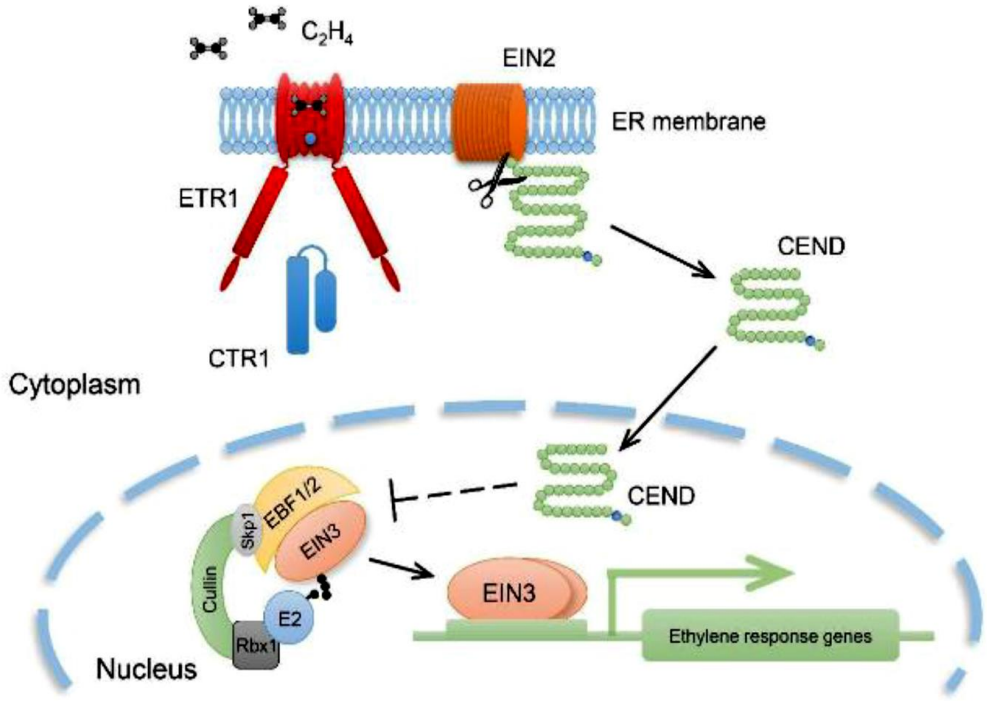

Fig 2. Model of EIN2 action in the ethylene signaling pathway [25]

Through this recovery chemical reaction methyl group can be kept preserve for the next round of ethylene production. In this way ethylene production can be continued for longer time without any shortage or demand of extra methionine. Simultaneously, the sulfur group belonging to methionine can also be preserved. At the end of the whole process, ACC oxidase enzyme oxidizes ACC to produce ethylene, CO_2, and cyanide. The cyanide is further detoxified to ß-cyano alanine using ß-cyano alanine synthase (ß-CAS, EC 4.4.1.9) in order to avoid any danger from toxicity of greater cyanide produced during higher ethylene synthesis reactions.

The rate-limiting step during biosynthesis of ethylene synthesis is considered to be the conversion of *S*AdoMet to ACC by utilizing ACC synthase. Findings that transcript level of ACS genes is immensely modulated with different signals and also that active ACC synthase is labile and available at minute levels solidly explains the tight control of ethylene biosynthesis process. Various plant species have been reported for both positive and negative feedback modulation of ethylene biosynthesis [26, 27]. Different ACS isoforms are the basic targets during ethylene biosynthesis phenomena. For instance, in case of *Solanumlycopersicum*, Le-ACS6 is negatively, and Le-ACS2 and Le-ACS4 are positively modulated in tomato due to the ethylene synthesized in course of fruit ripening process. Scientist has over the years tried to understanding the ACS regulation in different plant species, focusing on the expression pattern of ACS genes in reply to a range of endogenous signal and environmental stimuli. The unanimous fact recorded is that the ACS enzymes are regulated through a spatial and temporal mechanism and various internal and external cues are modulating its activities in plant body.

Ethylene signaling

Research approach over the years has explained one fact that ethylene signaling pathways is a combination of expanding complex signaling network which comprise of many regulation and feedback pathways. Biosynthesis of any bio-chemical compound is followed by the phenomena of signaling and mode of action through its specific functioning body. So followed by ethylene synthesis, now ethylene has to be perceived and its signals can be properly transduced via complex transduction machinery in order to stimulate certain biological responses. Couple of mutants weakened as a result of their response to ethylene is identified, utilizing the well-discovered reproducible triple response in case of dark-grown Arabidopsis seedlings. Functional analysis, characterization and cloning of genes found to get disturb or altered in these mutants are helping to portray an overall image of ethylene signal transduction pathway.

Ethylene signaling towards the senescence associated incidences

It has been reported that regulation of plant hormones acts as endogenous signals in almost all prospectus of plant growth and development, including senescence. Ethylene, Abscisic acid (ABA), Auxins, Cytokinins, Gibberellin (GA), Jasmonic acid (JA), all have and vital roles in promoting or inhibiting senescence approach [28-30] Mentioned below is a concise depiction of the effects of presented hormones on flower and leaves senescence

In ethylene-sensitive flowers, senescence is accompanied by a sudden and transient increase of respiration associated with an upsurge in ethylene production [30]. In many species pollination hastens the senescence-associated events inducing a rise of ethylene production [31, 32]. In *Dianthus caryophyllus*, exposure to ethylene resulted in premature petal senescence and increased or reduced the abundance of mRNA populations, suggesting that changes in petal physiology may be the result of rapid changes in gene expression [33]. The pattern of ethylene production in carnation flowers during the vase life and in response to exogenous ethylene and the expression of one ACC oxidase gene and two ACC synthase genes were investigated. Increased expression of these genes was observed during natural senescence as well as a rapid induction by ethylene treatment [34] In cut rose, flower opening is regulated by ethylene through the expression in petals of two receptors and two *CTR* genes, and the application of exogenous ethylene induced expression of *Rh-ETR* genes [35]. The importance of ethylene biosynthesis and perception has been emphasized using transgenic plants with up- or down-regulation of key biosynthetic genes. *Petunia x hybrida*over-expressing the antisense *BoACS1* gene (ACC synthase) or the antisense *BoACO1* gene (ACC oxidase) from broccoli showed reduced ethylene biosynthesis and delay of flower senescence [36].The over-expression of the *Arabidopsis ETR1-1* gene delayed DNA fragmentation and nuclease *PhNUC1* gene expression in *Petunia* flowers [37], and delayed flower and leaf senescence and increased the flowering time in tobacco and *Campanula carpatica*respectively [38, 39]. Cited studies revealed the how endogenous and exogenous ethylene production can influence the flower opening and flower senescence. Flowers and ornamental plants can be categorized into two types of plants depending on their response. Flowering and senescence of such plants are closely related to ethylene. On the other hands, plants amaranth, chrysanthemum, asparagus, mainly grouped in the lily family and Araceae are categorized as non-climacteric plants where the flowering and senescence stages are ethylene-insensitive [40].

ERF genes constitute as one of the largest transcription factor gene family of the plants.

Ethylene responsive element binding factor (ERF) genes represented as one of the leading transcription factor gene families in plants. While, up till now in Arabidopsis and rice, only a few ERF genes have been characterized. Flower senescence is associated with increased ethylene production in many flowers. However, the characterization of ERF genes in flower senescence has not been reported. Based on the sequence characterization, the PhERFs could be classified into four of the 12 known ERF families. Their predicted amino acid sequences exhibited similarities to ERFs from other plant species. Expression analyses of PhERF mRNAs were also been performed and genes of group VII showed a strong association with the rise in ethylene production in both petals and gynoecia, and might be associated particularly with flower senescence in petunia [41]. Even though, it also examined that Arabidopsis genome contains a large number of putative transcription factors, which containing a DNA binding domain similar to APETALA2/ethylene response element binding protein (AP2/EREBP), for most of which a function is not known. Phylogenetic analysis divides the APETALA2 (AP2) super-family into 5 major groups; AP2, RAV, ethylene response factor (ERF), dehydration response element binding protein (DREB) and At4g13040 Similar to ERF and DREB.

Moreover, ethylene response factors (ERFs) are plant transcriptional regulators mediating ethylene-dependent gene expression via binding to the GCC motif found in the promoter region of ethylene regulated genes. It has been reported on the structural and functional characterization of the tomato Sl-ERF2 gene that belongs to a distinct class of the large ERF gene family. Over-expression of the Sl-ERF2 gene in transgenic tomato lines results in premature seed germination and enhanced hook formation of dark grown seedlings, which is indicative of increased ethylene sensitivity. Whilst, [42] studied that genes in the ERF family encode transcriptional regulators with a variety of functions which involved in the developmental and physiological processes in plants. However, comprehensive computational analysis identified total of 122 and 139 ERF family genes in Arabidopsis (Arabidopsis thaliana) and rice (Oryza sativa L. subsp. Japonica), respectively. A complete overview of this gene family in Arabidopsis is presented, including the gene structures, phylogeny, chromosome locations, and conserved motifs. In addition, a comparative analysis between these genes in Arabidopsis and rice was performed. As a result of these analyses, the ERF families in Arabidopsis and rice were divided into 12 and 15 groups, respectively, and several of these groups were further divided into subgroups.

Ethylene Responsive Factor (ERF) response to different stress conditions

ERF family transcription factor, tomato (Solanumlycopersicum) ETHYLENE-RESPONSIVE FACTOR 52 (SlERF52) [43] is specifically expressed in pedicel abscission zones (AZs) and SlERF52 expression is suppressed in plants with impaired function of MACROCALYX and JOINTLESS, which regulate pedicel AZ development. RNA interference was used to knock down SlERF52 expression to show that SlERF52 functions in flower pedicel abscission. When treated with an abscission-inducing stimulus, the SlERF52-suppressed plants showed a significant delay in flower abscission compared with wild type. They also showed reduced up regulation of the genes for the abscission-associated enzymes cellulase and polygalacturonase. SlERF52 suppression also affected gene expression before the abscission stimulus, inhibiting the expression of pedicel AZ-specific transcription factor genes, such as the tomato WUSCHEL homologue, GOBLET, and Lateral suppressor, which may regulate meristematic activities in pedicel AZs. These results suggest that SlERF52 plays a pivotal role in transcriptional regulation in pedicel AZs at both pre-abscission and abscission stages. While a gene encoding putative ethylene response factor of AP2/EREBP family from cotton (Gossypiumhirsutum) showed that GhERF12 protein contains a central AP2/ERF domain (58 amino acids) with two functional conserved amino acid residues (ala14 and asp19). Transactivation assay indicated that GhERF12 displayed strong transcription activation activity in yeast cells, suggesting that this protein may be a transcriptional activator in cotton. Quantitative RT-PCR analysis showed that GhERF12 expression in cotton was induced by ACC and IAA. Overexpression of GhERF12 in Arabidopsis affected seedling growth and development. The GhERF12 transgenic plants grew slowly, and displayed a dwarf phenotype. The mean bolting time of the transgenic plants was delayed for about 10 days, compared with that of wild type. Further study revealed that some ethylene-related and auxins-related genes were dramatically up-regulated in the transgenic plants, compared with those of wild type. Collectively, we speculated that GhERF12, as a transcription factor, may be involved in regulation of plant growth and development by activating the constitutive ethylene response likely related to auxin biosynthesis and/or signaling [44].

Ethylene Responsive Factor (ERF)

A computational examination revealed 122 and 139 ERF family genes in model plant Arabidopsis thaliana and Oryza sativa L. subsp. japonica, respectively. Ethylene response factor (ERF) family involves genes that encode a variety of transcriptional regulators having a range of functions and keenly engaged in the physiological and developmental processes in plant body. ERF gene family has been studies and over viewed with great details in

Arabidopsis over the period of time, including the gene structures, chromosome locations, conserved motif and phylogeny, chromosome locations. In addition, a comparative analysis between these genes in Arabidopsis and rice was performed. On the other hand, few of the groups/subgroups were species specific. Furthermore, it was formulated that further widening of ERF family in plant species is due to chromosomal and tandem duplications, and also primitive transposition and homing are also playing their parts. These results are generalized for the effective functional analyses of ERF family genes.

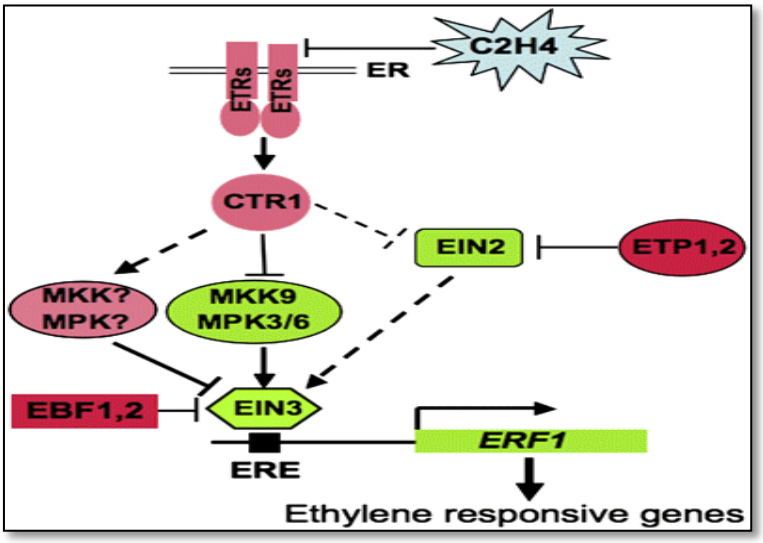

Fig 3. Ethylene Responsive Factor (ERF) prospective

Conclusion and future prospective

In order to meet the challenges of increasing population of the world, there is an insistent need to boost crop yield. Roses are the famous ornamental crops as both domestic and commercial cut flowers. Rose plant varies in shape, color and size ranging with compact, miniature roses, and rose with climbing nature called climbers that can attain a height of 7 meters. Significant quantities of flowers are magnificent quality and quantity of rose and other ornamental flowers are grown in most of the tropical countries of the world, and then these flowers needs to transport to far distinct places via ships, or air. Unlike other phytohormones, ethylene is gaseous in nature and only member of its class. It holds a simple structure if compared to the rest of the plant growth substances. Ethylene is normally generated by higher plants and is usually linked to fruit ripening and specific triple response. Generally, all kinds of biotic and abiotic stresses including temperature fluctuations, water imbalance, salt issues, pathogen or insect attacks holds certain specific kind of negative influence on the plants growth and development. In this matter of concern, nature has always behaved in an adoptive approach and the in case of these environmental or internal cues, plants have adopted various kinds of defense mechanisms in order to perceive stimuli from the surroundings and then conductively react these various stresses by changing the transcript levels of specific responsive genes [45]. Transcription factors are known for their crucial functions in signal transduction to trigger or repress expression of defense gene, along with in the modulation of connectivity among various signaling pathways [46]. ERF genes are observed to be stimulated not only with disease-concerned and pathogen infection stimuli, but its expression levels can also be trigger due to abiotic stresses, thus in this way ERF genes like Rh ERF can improve the multiple stress resistances in the transgenic plants. Furthermore, over-expression study analysis of ERF gene revealed that these transcription factors can bring a broad-spectrum resistance towards pathogens and other abiotic stresses and can also the tolerance in transgenic plants towards drought, salt, and freezing. Thus, Rh ERF gene are focus under this specific research study in order to explore its role in flower opening in relation to abiotic stress such as ethylene stimuli.

A family of five membrane localized receptors is responsible to perceive the ethylene. These receptors are homologous with the bacterial two-component histidine kinases engaged in recognizing various environmental alterations happening. The network generally holds two kinds of proteins: a histidine kinase which act as a sensor and auto phosphorylates the internal histidine residue in reaction to environmental cues, and the second protein is the response regulator which is playing a role as to activates the downstream components when it receives a phosphate from histidine residue of the sensor on its own aspartate residue [47]. Arabidopsis has been found with five ethylene receptors: ETR1, ETR2, ERS1, ERS2, and EIN4 [48,49]. Only ETR1, ETR2 and EIN4 receptors among the total five receptors comprised of the receiver domain which are same to the bacterial response

regulators present at the C-terminal of the structure of protein.

Each of these above mentioned receptor contains an N-terminal membrane-spanning domain which can play its role in a way that when the ethylene is perceived, these domain can binds the ethylene to a copper cofactor, which is supplied by a RAN1 copper transporter [50]. Yet an in- vitro display of protein kinase activity is shown by the receptors, but the biochemical signaling phenomena is still to be discovered [51]. The receptors focused here in this case are negative regulators of ethylene signaling based on the genetic approach [52]; so in case of absence of ethylene, these localized receptors repress downstream ethylene responses via another mechanized group of proteins known as Raf-like protein kinase CTR1 [53], and when ethylene got attached then in this case the receptors are no more continue to repress ethylene responses [54]. The positive regulator EIN2 is repressed by CTR1, thus CTR1 is basically negatively regulating the ethylene responses [55]. Subsequently the ethylene signaling is communicated to the transcription factors EIN3 and EILs through an unknown mechanism, which in reaction activates another important transcription factor ERF1 [56]. Furthermore, Ethylene Responsive Factor (ERF1) can trigger the transcription activity of some of the ethylene responsive genes including PDF1.2. A proper mechanized pathway known as 26S proteasome-dependent pathway is used to control EIN3 and EIL1 which are constitutively expressed [57]. The whole phenomena and mechanism of ethylene signaling are preserved between dicot and monocot [58].

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