Review

Role of ethylene and the APETALA 2/ethylene response factor superfamily in rice under various abiotic and biotic stress conditions

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ABSTRACT

Ethylene, the simplest gaseous plant growth regulator (PGR), controls diverse physiological pathways in plants. Under various stress conditions and during different developmental stages, such as root elongation, leaf and flower senescence, seed germination, tissue differentiation and organ abscission, ethylene biosynthesis is significantly increased. In rice, the internal ethylene concentration is rapidly regulated to a genetically, physiologically and morphologically relevant level under various stresses. Regulation of the ethylene signalling pathway under adverse conditions results in up- and/or down-regulation of the expression of stress-related genes in different families. Transcription factors are proteins that influence and control a number of biological processes under both normal and stress conditions. APETALA 2/ethylene response factor (AP2/ERF) is a transcription factor that is considered to function in stress response pathways in rice. To date, many AP2/ERF genes have been functionally characterised in rice. An understanding of the interactions between the AP2/ERF genes and ethylene-dependent mechanisms may provide new insights to facilitate the enhanced adaptation of rice to stress. In the current review, the structure and function of ethylene in rice under normal and stress conditions are described, and then the general functions of the plant AP2/ERF transcription factors are discussed. In addition, the interactions between the AP2/ERF genes and ethylene pathways under abiotic stresses, including submergence, cold, salinity, drought and heavy metal stresses, as well as those under biotic stresses, are summarised. Although the AP2/ERF genes have been identified, information on the physiological mechanisms of this gene family under stress conditions in rice remains limited. Therefore, further physiological studies must be performed in the future to identify additional features of this crucial gene family.

Contents

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1. Introduction

Ethylene (ET) is a gaseous phytohormone involved in various processes that are required for plant germination, growth and development (Ju and Chang, 2015; Schaller and Voesenek, 2015). This phytohormone either induces or inhibits its own synthesis in a process termed "autoinduction" or "autoinhibition", respectively (Donnell et al., 1996). At an optimum concentration and with appropriate timing, the application of ET promotes agricultural production by enhancing the growth of treated crops. In addition, the combined application of ET with other hormones, such as cytokinin and auxin, allows for regulation of the ethylene level and further enhances agricultural production (Müller and Munné-Bosch, 2011; Bakshi et al., 2015). Further, the application of ethylene to field decreases production cost considerably as it reduces the fruit removal force, which can diminish the damage rate during mechanical harvesting. This gaseous hormone can be applied to a wide variety of plants for manipulation of harvesting during the daytime (Cohen and Kende, 1986). It has also been reported to regulate plant biological mechanisms in response to various abiotic (submergence, drought, salt, flooding, and cold) and biotic (insect, fungal, and microbial infections) stresses (Donnell et al., 1996; Broekaert et al., 2006; Van Loon et al., 2006; Grennan, 2008; Müller and Munné-Bosch, 2015). Depending on the adverse conditions, it acts as either a positive or negative modulator (Yoo et al., 2009).

In rice, the ethylene signalling cascade involves a variety of transcription factor families. The regulation of stress-responsive genes by transcriptional regulatory factors, also known as transcriptome reprogramming, is a critical step in the development of rice responses to a wide spectrum of environmental stresses. To date, multiple regulatory transcription factors that are necessary for transcriptome reprogramming under detrimental conditions have been identified and functionally analysed. These transcription factors have been classified into various superfamilies, and the APETALA 2/ethylene-responsive element binding factor (AP2/ERF) superfamily is one of the largest transcription factor superfamilies in crops (Singh et al., 2002). The interactions between ethylene and this superfamily may play significant roles in the regulation of physiological processes under normal and detrimental conditions (Müller and Munné-Bosch, 2015). Therefore, functional evaluation of the ethylene signalling network that involves the AP2/ERF superfamily may facilitate the determination of how ethylene modulates adaptive stress responses in plant (Rzewuski and Sauter, 2008). Previous investigations on the ethylene and AP2/ERFs role under diverse conditions have mainly focused on dicotyledonous plants such as *Arabidopsis*, tobacco and tomato. However, relevant studies in monocotyledonous species, such as rice have not been systematically summarised. To the best of our knowledge, this is the first report on some intriguing aspects of ethylene interaction with AP2/ERF family members related to adaptive responses of rice to different environmental conditions.

2. Physio-molecular pathway of ethylene biosynthesis in rice

S-adenosylmethionine (AdoMet) is a primary amino acid component of the ethylene biosynthesis pathway. In the first committed step of ethylene biosynthesis in rice, AdoMet is converted into 1-carboxylic acid (ACC) and a by-product, 50-methylthioadenosine, in a reaction catalysed by 1-amino-cyclo-propane-1-carboxylic acid (ACC) synthase (ACS) (Fig. 1) (Rzewuski and Sauter, 2008). ACS belongs to a family of proteins (PLP-dependent enzymes) that require a cofactor (pyridoxal-5′-phosphate). This enzyme catalyses elimination, carboxylation, deamination, transamination or replacement of the γ and β carbons of amino acids (Argueso et al., 2007). ACS is induced by various developmental and environmental factors via different gene families in rice (Yamagami et al., 2003; Tsuchisaka and Theologis, 2004). Based on their C-termini, three types of ACS proteins regulated by a small multigenic family have been identified in rice (Iwai et al., 2006). Type-1 ACS proteins have the longest C-termini and contain a conserved Ser that is a phosphorylation site for calcium-dependent protein kinase (CDPK), in addition to three Ser residues that are potentially phosphorylated by the mitogen-activated protein kinase MPK6 (Tatsuki and Mori, 2001; Sebastià et al., 2004). In addition, type-2 ACS proteins include the Ser phosphorylation site for CDPK, and type-3 ACS proteins possess the shortest C-termini and lack phosphorylation sites (Rzewuski and Sauter, 2008).
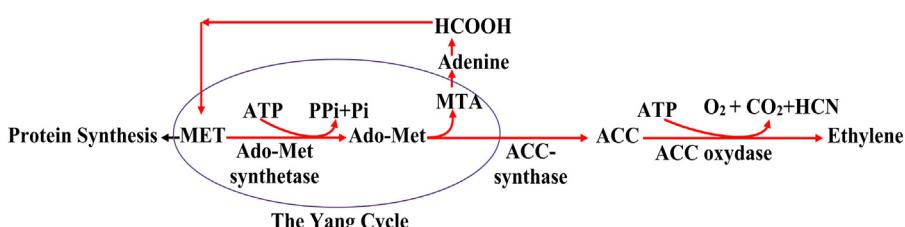
Fig. 1. The ethylene biosynthetic pathway in rice. The enzymes that catalyse each step are shown under the arrows. AdoMet: AdoMet synthetase produces AdoMet at the expense of ATP; Met: methionine; ACC: 1-aminocyclopropane-1-carboxylic acid; and MTA: methylthioadenine. MTA is recycled back to methionine through the Yang cycle, successively involving MTA nucleosidase. ACC and MTA are released in each reaction (Argueso et al., 2007).

The second step of ethylene biosynthesis is catalysed by the ACC oxidase (ACO) enzyme. Expression of the ACO gene and its multiple isoforms has been shown to be strongly correlated with the concentration of ethylene under different environmental conditions and developmental stages (Ruduś et al., 2013). In this step, dioxygen and ACC are metabolised to cyanide, CO_2 and ethylene (Fig. 1) (Cohen and Kende, 1986; Chen et al., 2002). ACO belongs to a group of ferrous-dependent nonheme oxygenases that are encoded by a small multigene family. Computational analysis has revealed that the rice genome contains six ACO (OsACO1-6) genes (Iwai et al., 2006). However, only three ACO gene paralogues (OSACO1-3) have been identified according to the Rice Genome Annotation Project database (Ouyang et al., 2007). In rice, OsACO1 was the first ACO gene to be isolated, and it is most highly expressed in the young growing internode in response to submergence (Mekhedov and Kende, 1996). In addition, OsACO2 and OsACO3 are expressed at the highest levels in seedlings, in which they are regulated by auxin and ethylene, respectively, in a concentration-dependent manner (Chae et al., 2000).

As mentioned above, methylthioadenosine is produced as a by-product in the ethylene biosynthesis pathway. However, the concentration of ethylene exceeds that of methionine in plant tissues. Thus, in the ethylene synthesis pathway, methionine must be recycled in the Yang cycle, which metabolizes MTA to produce AdoMet (Fig. 1) (Baur and Yang, 1972; Rzewuski and Sauter, 2008). MTA is hydrolysed to adenine and methylthioribose (MTR) via MTA nucleosidase in plants. Then, MTR kinase phosphorylates MTR (MTR-phosphate) (Yang and Hoffman, 1984; Miyazaki, 1987). Acireductone is activated by dehydratase/enolase–phosphatase and the isomerase activity of MTR-P. The acireductone dioxygenase enzyme requires the binding of metal ions to catalyse two enzymatic reactions involving the same substrate. Fe-ARD catalyses the Yang cycle reaction, whereas Ni-ARD catalyses an off-pathway reaction to produce methylthiopropionate, formate and carbon monoxide. Acireductone produces 2-keto-4-methylthiobutyrate in a reaction catalysed by acireductone dioxygenase. Then, 2-keto-4-methylthiobutyrate is transaminated to yield methionine. Finally, methionine is converted to AdoMet by S-adenosylmethionine synthetase (SAMS) using ATP as a substrate (Fig. 1) (Rzewuski and Sauter, 2008). The ethylene biosynthesis pathway in rice involves five SAMS-encoding genes (OsSAM1-5), two related MTR kinase-encoding genes (OsMTK1-2), two ARD-encoding genes (OsARD1-2) and OsMTN as an MTA nucleosidase-encoding gene (Rzewuski and Sauter, 2008).

3. The stimulus-response mechanism of the ethylene biosynthesis pathway in rice

Physiological analysis of rice has revealed that environmental and hormonal stimuli are sensed by a two-component regulatory system (Chang and Stewart, 1998). The basic two-component signalling pathway is composed of histidine kinases and histidine-containing phosphotransfer proteins (HPKs), as well as a response regulator (Schaller et al., 2011). Histidine kinase is a transferase protein that plays a regulatory role in this two-component signal transduction system across the cellular membrane (Bilwes et al., 1999; West and Stock, 2001). In plants, two-component receptor kinases sense and respond to ethylene stimulus (Rzewuski and Sauter, 2008). The rice ethylene signalling components have been shown to recognize different receptor molecules, such as an ETHYLENE INSENSITIVE 3 (EIN3) orthologue, EIN2, EIN5, EBF1/2, RTE1 and CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1 homologues) (Rzewuski and Sauter, 2008).

Ethylene receptors are stimulated by hormones, as well as biotic and abiotic stresses (Watanabe et al., 2004). In rice, five genes encoding ethylene receptors have been identified. These genes belong to subfamilies I (OsERS1 and OsERS2) and II (OsETR2, OsETR3, and OsETR4) (Rzewuski and Sauter, 2008; Yan et al., 2013). Ethylene receptors possess similar modular structures, containing three conserved transmembrane domains near the N terminus, followed by a GAF domain, and signal output motifs in the C-terminal half (Hall et al., 2012). It has been reported that subfamily I members have the GAF domain (cGMP phosphodiesterases/adenylyl cyclases/FhlA) and lack the C-terminal histidine kinase domain, whereas subfamily II receptors contain both the GAF and C-terminal histidine kinase domains (Yau et al., 2004).

CONSTITUTIVE TRIPLE-RESPONSE1 (CTR1) is an important mediator of ethylene receptor signal output in rice. To date, three CTR genes (OsCTR1-3) have been reported in rice, of which OsCTR1 and OsCTR2 are more closely related to CTR1 (Wang et al., 2013). These three CTRs act downstream of ethylene receptors and upstream of EIN2. Rice CTR1 is encoded by multiple CTR-like genes (Ramina et al., 2007). Rice also possesses four genes that encode the EIN2 protein (OsEIN2/MHZ7, OsEIN2.2, OsEIN2.3 and OsEIN2.4) (Ma et al., 2013). In the absence of ethylene, active receptors negatively regulate EIN2 through phosphorylation via the protein kinase CTR1. Upon ethylene perception, the receptors become inactivated, which in turn facilitates EIN2 activation to mediate ethylene signalling (Merchante et al., 2013). Upon activation, the C-terminal part of EIN2 is cleaved off and travels to the nucleus to mediate ethylene signalling via EIN3 and EIN3-LIKE1 (EIL1) (Rzewuski and Sauter, 2008; Wen, 2015). Six EIN3-like homologues (OsEIL1-6) have been identified in rice (Mao et al., 2006). In the ethylene signalling pathway, EIL1 and EIN3 have been reported to be central transcription factors that mediate ethylene signal transduction in the nucleus (Yang et al., 2015). Rice genome analysis has revealed that the EIN5, CTR1 and Ein3-binding F-box (EBF) genes act downstream of ethylene signalling between the receptor and nucleus (Rzewuski and Sauter, 2008; Zhang et al., 2009). In rice, two F-box proteins (OsEBF1-2) regulate the stability of EIN3/EIL1 via a 26S proteasome degradation network (Yang et al., 2015). Down-regulation of the expression of the EBF1-2 proteins by ethylene stabilises EIN3/EIL1 in the presence of EIN2 (An et al., 2010). EIL1 and EIN3 also regulate the expression of ethylene-responsive proteins, including transcription factor ethylene response factor1 (ERF1) (Chao et al., 1997; Wen, 2015). OsERF1 is a member of the ethylene response factor subfamily that is induced by ethylene in various rice organs. In Arabidopsis, OsERF1 overexpression has been demonstrated to regulate two ethylene-responsive genes, b-chitinase and PDF1.2, and to induce development of the ethylene-hypersensitive phenotype (Hu et al., 2008).

ERFs belong to the AP2/ERF superfamily, and in plants, they participate in the ethylene signalling pathway (Ma et al., 2014), as demonstrated by mutant complementation and transgenic studies. It has been reported that the ERF expression is regulated by ethylene at various concentrations exogenously and/or endogenously (Yang et al., 2015). Studies in which ethylene signalling networks have been engineered have recommended novel strategies for enhancing stress tolerance in rice. However, modifications of the up- and downstream mechanisms of the ethylene signalling networks may have detrimental effects on rice development. Overexpression of ethylene has been shown to regulate the expression of AP2/ERF, which indicates the acquisition of stress tolerance, without causing undesirable effects on rice development (Chen et al., 2012; Zhai et al., 2013). These results suggest that focusing on the ethylene-mediated induction of

AP2/ERF may be a good starting point for the genetic improvement of stress tolerance in rice (Kazan, 2015).

4. APETALA 2/ethylene-response factor, an influential superfamily in rice

The AP2/ERF supergene family is involved in various plant developmental processes, such as the control of seed size and weight, seed oil accumulation, germination, flowering and activation of wax biosynthesis, ripening and induction of protein synthesis, in different species (Zarembinski and Theologis, 1997; Jofuku et al., 2005; Jin et al., 2010). Based on the number of AP2/EREBP DNA-BDs and their sequence similarity, Sharoni et al. (2011) identified 167 AP2/ERFs in rice, which could not be used to construct an acceptable phylogeny due to the presence of very small motifs in four out of the 167 genes (LOC_Os12g41040, LOC_Os05g28800, LOC_Os03g06920 and LOC_Os12g40960). In addition, Rashied and colleagues (Rashid et al., 2012) classified 170 AP2/ERF genes into 11 groups, including the following four main groups: APETALA 2 (AP2), Ethylene-Responsive Factor (ERF), Related to ABI3 and VP1 (RAV) and Dehydration-Responsive Element-Binding proteins (DREBs); these genes were further classified into 10 subgroups, and two genes were identified that did not belong in any group (Rashid et al., 2012). The proteins in the four subfamilies of the AP2/ERF family contain approximately 60–70 amino acids each, and they each form a typical three-dimensional structure, with a layer of three antiparallel beta-sheets, followed by a parallel alpha helix (Allen et al., 1998). Reportedly, the ERF and DREB subfamilies possess a single AP2/ERF domain, whereas the AP2 subfamily contains two repeated AP2/ERF domains. In contrast, RAV possesses an AP2/ERF domain and a B3 domain (Kagaya et al., 1999), and in seed plants, AP2 subfamily proteins contain either an ANT or AP2 domain (Mizoi et al., 2012).

This superfamily regulates plant transcription in response to detrimental conditions (Shinozaki and Yamaguchi-Shinozaki, 2007), and ERFs and DREBs are two prominent subclasses. To date, several abiotic stress-inducible DREB genes have been identified. This subfamily includes DRE-binding proteins (A/GCCGAC) and DRE-like cis-elements that activate abiotic stress-responsive gene expression by binding to the dehydration-responsive element/C-repeat (DRE/CRT) cis-acting elements in their promoters (Stockinger et al., 1997; Liu et al., 1998). DREBs activate various dehydration- and cold-regulated (RD/COR) genes through interactions with the DRE/CRT elements (A/GCCGAC) in these genes. The activation of RD/COR proteins enables plants to respond to low temperatures and water deficit (Stockinger et al., 1997; Liu et al., 1998; Solano et al., 1998; Lucas et al., 2011; Xu et al., 2011). The binding of ERF to the AGCCGCC (i.e., GCC box) sequence has been widely investigated. GCC boxes have been detected in the promoters of several pathogenesis-related genes (Eyal et al., 1993; Ohme-Takagi and Shinshi, 1995; Zhou et al., 1997). Interestingly, evidence indicates that flanking sequences affect the binding of ERFs to the GCC box (Tournier et al., 2003; Gao et al., 2007). This evidence verifies the regulatory effects of the GCC box on the transcriptional activation of pathogenesis-related genes, such as osmotin (PR5), chitinase (PR3), chitinase (PR3), β-1, 3-glucanase (PR2) and prb-1b (PR1), under biotic stress (Ohme-Takagi and Shinshi, 1995; Büttner and Singh, 1997; Alonso et al., 1999; Zarei et al., 2011). These findings are further supported by the observation of the high binding activities of ERFs to the GCC box motif in the promoter region of a nuclear gene encoding a class I 1,3-glucanase in bacterial-infected plants (Alonso et al., 1999). All of the above-mentioned results strengthen the notion that ERFs bind to the GCC-box (GCCGCC) to regulate the expression of pathogenesis-related (PR) genes (Ohme-Takagi and Shinshi, 1995; Büttner and Singh, 1997).

5. Regulation of ethylene in abiotic and biotic stress tolerance by modulating the expression of AP2/ERF transcription factors in rice

The relationship between ethylene and AP2/ERF expression in stress-induced signalling pathways regulates plants' adaptations and responses to detrimental conditions. However, depending on diverse factors, such as the type of stress (submergence, cold, salt, drought, heavy metal or biotic stress), the interaction of ethylene with the expression of AP2/ERF can dramatically differ.

6. Cross-talk between ERFs and ethylene in rice in response to submergence

Flooding is an occurrence or natural event characterised by an excess of water, such as that resulting from submergence or waterlogging (Peeters et al., 2002; Sasidharan and Voesenek, 2015). The synergistic or antagonistic functions of different PGRs indicate that ethylene plays roles in the acclimatory responses to flooding and submergence in rice (Fukao et al., 2009). Under hypoxia, ethylene regulates cell death, leading to the formation of adventitious roots and aerenchyma, as well as the induction of petiole and internode elongation. As a result of these changes, the photosynthetic organs of rice extend above the water surface (Gunawardena et al., 2001; Voesenek et al., 2006). Investigations of the rice metabolic network under anoxic conditions have revealed that ET is a normal product of anaerobic respiration (Horton, 1991). Due to the slower rate of ethylene diffusion in water than in air, the ethylene concentration rapidly rises in rice, thereby promoting the initiation of mesocotyl, leaf, coleoptile, internode and petiole elongation under submerged conditions (Kendrick and Chang, 2008).
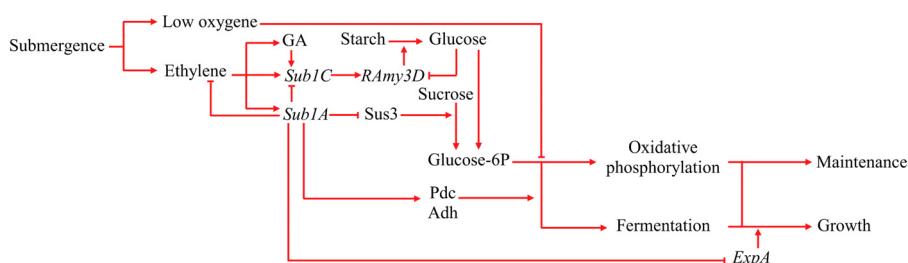
Fig. 2. Schematic model of the link between ethylene and gene expression under submergence in rice. The *Sub1A* gene is expressed in the ethylene signalling cascade under submergence stress. Sucrose synthase and Expansin A are repressed by *SUB1A*. *SUB1A* enhances the enzymatic activities of alcohol dehydroxygenase (Adh) and pyruvate decarboxylase (Pdc), as well as the accumulation of their mRNAs. To provide energy for survival under such conditions, fermentation allows for the continuation of glycolysis and the synthesis of ATP. The degradation of starch provides glucose for both growth and glycolysis. *Sub1A* also represses *SUB1C*. *SUB1C* controls the *Ramy3D* gene (a-amylase gene). Additionally, *Sub1C* is regulated by gibberellins (GAs) (Fukao et al., 2006; Perata and Voesenek, 2007).

The quiescence strategy is another pivotal concept that has enabled plants to adapt to submergence (Bailey-Serres and Voesenek, 2008). The mechanism is characterised by the inhibition of rice elongation during flooding and its subsequent re-growth when the water recedes. Recent molecular and genomic analyses have identified a quantitative trait locus designated as Submergence 1 (*Sub1*) using this strategy (Xu et al., 2006). At the transcript level, expression of the ERF genes, including *Sub1C* and *Sub1A*, is controlled by ethylene and submergence (Fukao et al., 2009). *Sub1A* primarily promotes submergence tolerance in lowland rice, and *Sub1B* and *Sub1C* are regulatory factors that are induced in a wide variety of *Japonica* and *Indica* rice cultivars (Fukao et al., 2006). All three of these *Sub1* genes belong to the B-2 subclass of ethylene response factors (ERFs)/ethylene-responsive element proteins, which possess a single 58- to 59-residue ERF domain (Gutterson and Reuber, 2004). While the *Sub1A* gene down-regulates the expression of B-2 subgroup genes, it up-regulates that of diverse A-1 (DREB1/CBF) subgroup genes in the DREB subfamily, as well as that of B-1 and B-2 subgroup genes in the ERF subfamily. SNORKEL1 and 2 (*SK1* and *SK2*) are additional *Sub1A*-related genes in deepwater rice that are involved in ethylene-induced internode elongation during hypoxia, flooding and submergence (Hattori et al., 2009). Analysis of the Sub locus has resulted in the identification of two alleles of *Sub 1A,* namely *Sub1A-1* (tolerance-specific allele) and *Sub1A-2* (intolerance-specific allele). Following transfer of the *Sub1A-1* allele into submergence-intolerant rice, the down-regulation of *Sub1C* expression has been observed, in addition to the up-regulation of alcohol dehydrogenase 1 (*Adh1*) expression (Fig. 2). The presence of *Sub1A-1* at the Sub1 locus indicates that ethylene and GA negatively regulates carbohydrate consumption and cell elongation and positively regulate ethanolic fermentation during submergence. These results indicate that *Sub1A-1* overexpression enhances the submergence tolerance and crop security of transgenic rice. Interestingly, the absence of *Sub1* genes at the Sub1 locus has been observed in some deepwater rice (Perata and Voesenek, 2007; Jung et al., 2010; Fukao et al., 2011).

7. Interactions of ethylene with ERFs in response to cold stress in rice

Freezing and low temperatures pose serious risks to the sustainability of plant productivity. The reported negative effects of cold stress on rice include stunted seedling growth, poor germination, reduced leaf expansion, the yellowing of leaves (chlorosis) and wilting. The final consequence of these effects is tissue death (necrosis) (Xiong et al., 2002; Bajaj and Mohanty, 2005; Roy et al., 2011; Thirugnanasambantham et al., 2015). Cold acclimation is one of the most useful plant mechanisms that

function in the responses to low temperature and freezing (Kocsy et al., 2001). The cold signalling pathway regulates the expression of various genes involved in the mechanisms of action of plant phytohormones, including ethylene, salicylic acid and abscisic acid (Yadav, 2010). Although previous studies have emphasised the functions of ABA-dependent pathways in cold signalling, recent studies have described regulatory functions of ABA-independent networks (Shi et al., 2012). Reportedly, the ethylene level is altered during cold stress in rice (Kocsy et al., 2001).

Genomic and molecular analyses of ABA-independent networks have revealed various transcriptional regulatory pathways that are involved in the modulation of stress-regulated genes (Agarwal et al., 2006). The transcriptional regulatory network is crucial for controlling the expression of cold-regulated genes (COR) under cold stress in rice. The expression of DREBs and ERFs is induced by ABA-independent pathways in response to cold stress (Lata and Prasad, 2011; Dey and Vlot, 2015). DREBs are classified into the DREB1/CBF and DREB2/CBF subfamilies (Liu et al., 1999), which play roles in different stress signalling cascades, including those involved in the cold and dehydration responses (Agarwal et al., 2006). Although expression of the *DREB1* gene has been extensively studied in many plants under abiotic stresses, few investigations have focused on *DREB2* expression in response to various stresses (Liu et al., 1999). The DREB1/CBF subfamily members are expressed in response to cold stress, and when their expression is ectopically induced, they improve plant tolerance to freezing and cold (Liu et al., 1999). Various regulatory genes, such as *DREB1B/CBF1*, *DREB1C/CBF2* and *DREB1A/CBF3*, are rapidly expressed within 15 min at low temperatures. Their gene products then induce the expression of downstream genes by binding to the RT/DRE regulatory factors in their promoters (De Paepe and Van Der Straeten, 2005). While expression of the genes encoding DREB subfamily members is promoted in response to abiotic stress, that of the *OsDREB1B* and *OsDREB1A* genes is not induced in rice exposed to ABA. Nonetheless, these genes have been reported to be expressed within 40 min under cold stress (Dubouzet et al., 2003). The ACC gene, which regulates ethylene production and activity, is up-regulated following overexpression of the *OsDREB1A* gene in transgenic rice (Ito et al., 2006). In contrast, in rice under dehydration and salinity (25 mM) stress, *OsDREB2A* expression has been detected after 24 h, with slightly increased expression in response to cold stress and ABA. In contrast, *OsDREB1C* has been shown to be constitutively expressed, and no *OsDREB1D* expression has been detected in the presence or absence of stress (Dubouzet et al., 2003). In accord with these findings, Haake et al. (2002) and Liu et al. (1998) have found that *DREB1B/CBF* and *DREB1C/CBF* are induced by cold. In contrast with the above-mentioned results, another study has reported that *DREB1A/CBF* is induced by cold, but not by salt or drought stress (Gao et al., 2007).

Table 1
The cold-dependent and independent ERF genes regulated by *OsMyb4* and various hormones (Park et al., 2010).

Rice ERF genes	Ethylene	ROS	ABA	JA	SA	Cold-mediated	Cold- independent	Up-regulated genes	Down-regulated genes
Os03g22170	√	√	√	√	√	√	–	ERD1-like and GCC-box-like	JAre-like
Os02g40070	√	√	√	√	√	√	–	ERD1-like and GCC-box-like	JAre-like
Os01g58420	√	√	√	√	√	√	–	ERD1-like and GCC-box-like	JAre-like
Os06g09717	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os01g04020	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os05g25260	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os06g42990	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os06g09390	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os04g46440	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os04g46400	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os02g54160	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os01g21120	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like
Os08g07440	√	√	–	√	√	–	√	–	ERD1-like and GCC box-like

Similar to *DREB1/CBF*, expression of the cold-induced signalling gene *OsDREBL* is promoted by ABA-independent pathways in rice. Additional studies have demonstrated that *OsDREBL* is expressed in response to low temperatures and cold and during the seedling stage in different parts of *Indica* and *Japonica* rice. The protein encoded by *OsDREBL* is present in the nucleus; however, it cannot bind to the DRE. Despite the similarity between the CRT/DREB box (TACCGACAT) and GCC-box of the response element (AGCCGCC), *OsDREBL* preferably binds to the GCC-box. These findings indicate that the above-mentioned genes only have roles in the responses to cold/low temperatures and that their products may bind to genes in the ethylene and cold-induced signal transduction networks (Chen et al., 2003). *TERF2/LeERF2* is another ERF family member (Zhang and Huang, 2010). In addition to the positive functions of TERF2 in the response to cold stress, this gene modulates the ethylene level in transgenic rice, tomato and tobacco. The TERF gene activates the expression of various cold-related genes, such as *OsICE1*, *OsLti6*, *OsMyb*, *OsCDPK7*, *OsFer1*, *OsSODB* and *OsTrx23*, in transgenic rice (Lorenzo et al., 2003; Zhang et al., 2004). In rice, *OsMyb* indirectly or directly controls its target genes via the intermediary NAC, ERF, ARF, MYB, bZIP and CCAAT-HAP transcription factors. In addition, *OsMyb4* increases the activities of the isoprenoid and phenylpropanoid metabolic pathways, including the ethylene, salicylic acid (SA), abscisic acid (ABA) and jasmonic acid (JA) pathways (Park et al., 2010). *OsMyb4* also up- or down-regulates the expression of various ERF genes in the ethylene signalling pathway in response to cold-dependent or independent signals (Table 1).

8. Ethylene and ERF performance in rice in response to salt stress

Salinity has negative impacts on plant growth and development (Chinnusamy et al., 2006). The two toxic ions Na^+ and Cl^- derived from NaCl can cause damage to plant cells through the induction of oxidative stress and osmotic stress, ion toxicity and nutrient deficiency (Gao et al., 2007; Talei et al., 2015). In rice, a high NaCl concentration results in a decreased growth rate, which may lead to plant death due to substantial changes in ROS levels, ion homeostasis and gene expression (Li et al., 2014; Talei et al., 2015). According to Zeng et al. (Zeng et al., 2002), the rice yield can decrease by up to 60% during growth at moderate salinity levels. In response to salinity, the expression of various genes in phytohormone networks is induced during plant growth and development (Thomashow, 1999). Salinity stress promotes ethylene biosynthesis, which can activate the downstream network and result in altered gene expression (Wang et al., 2002).

Based on investigations of transgenic and mutant lines, a sequence of the ethylene response under salinity stress has been elucidated. These investigations have confirmed that ethylene positively or negatively regulates salt tolerance (Cao et al., 2006; Peng et al., 2014). ACS, a rate-limiting enzyme, is the ideal target for the regulation of ethylene biosynthesis at both the transcriptional and post-transcriptional levels by salinity (Tao et al., 2015). Several ACS genes have been reported to be up-regulated under short- and long-term salinity stress in different monocotyledonous and dicotyledonous species (Achard et al., 2006). A more systematic study of the post-transcriptional levels of ACS genes showed that their expression was promoted by activation of WRKY mainly through induction of the mitogen-activated protein kinase (MAPK) cascade under salinity stress (Fig. 3) (Li et al., 2012). The MAPK cascades phosphorylate ACS proteins to prevent them from undergoing 26S proteasome-mediated degradation (Liu and Zhang, 2004). ACO is another ethylene biosynthesis target that is regulated by salinity. In response to salt accumulation, both the ACO activity and ACC content are increased to promote ET release
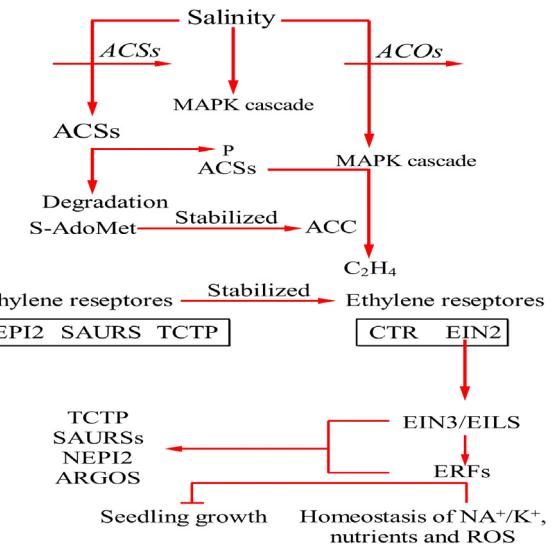
Fig. 3. Schematic model of the ethylene pathway under salinity in rice. During the salinity course, the MAPK phosphorylation pathways are activated by stress signals, and many ACS genes are stabilised by ACCs. In the next step, ACSs and ACOs, which are up-regulated in response to salinity, promote ethylene synthesis. To regulate several salinity response effectors, a salinity-induced ethylene signal is transduced via the classical EIN3-EIN2-CTR1 cascade. To enhance salinity tolerance, a proper level of ethylene promotes the homeostasis of ROS, Na^+/K^+ and nutrients. However, a higher ET concentration leads to the harmful hyper-inhibition of plant growth. To avoid the negative effects of an extreme ethylene response, crops have evolved negative feedback cascades to promote seedling growth and alleviate the ethylene response. In these cascades, a number of small proteins, including AtSAURs, NEIP2, AtARGOS and NtTCTP, act as key modulators to coordinate the ethylene/salinity responses and plant growth (Kiegerl et al., 2000).

(Kukreja et al., 2005). These findings further suggest that crops grown under salinity stress tend to synthesise an increased amount of ethylene mainly by enhancing ACOs and ACSs (Chen et al., 2014). Nonetheless, several other studies have reported that ACC may negatively regulate seedling growth in some plants under salinity stress (Albacete et al., 2009). While these results do not indicate that ACC has direct effects on the plant response to salinity stress, some reports have shown that ethylene is not the main plant growth inhibitor that is induced under these conditions (Shibli et al., 2007). It may be possible that ethylene plays a small, negative role in the crop response to salinity stress, at least during a certain growth stage (Tao et al., 2015).

Stress signals stimulate the biosynthesis of ET, which then binds to receptors, resulting in the inactivation of CTR1 and subsequently leading to EIN2 dephosphorylation and cleavage (Tao et al., 2015). The downstream transcription factors EIN3/EILs are stabilised by translocation of the C-terminus of truncated EIN2 into the nucleus (Qiao et al., 2008; Wen, 2015). In the ethylene cascade, ETP1/ETP2-mediated protein turnover regulates EIN2, and EBF1/EBF2-dependent ubiquitination regulates EIN3 (Guo and Ecker, 2003; Tao et al., 2015). At the end of the salinity stress-associated ethylene network, EIN3/EIL1 activates the transcription of downstream ethylene response factors, leading to the induction of ethylene responses (Guo and Ecker, 2003; Tao et al., 2015). In rice, ERFs are the key ethylene signalling factors that function downstream of EIN3. EIN3/EILs regulate and activate ERFs by binding to the promoter of ERF1 (Solano et al., 1998). In addition, SALT-RESPONSIVE ERF1 (*OsSERF1*) is activated by phosphorylation via *OsMAPK5* in rice. Interestingly, the *OsSERF1* and *OsMAPK5* transcripts are downstream targets of *OsSERF1* phosphorylation (Schmidt et al., 2013). Therefore, ERF1 is regulated and activated by a series of ethylene response genes, leading to a constitutive ethylene response (Fig. 3) (Solano et al., 1998). In rice, the functions

of other ERFs in the ethylene network in response to salinity stress have not yet been analysed.

9. Interactions between ethylene and ERFs in rice in response to drought

Drought and water deficit are the major natural hazards affecting plant production worldwide. They have many extremely deleterious effects on plant processes, including photosynthetic assimilation, nutrient metabolism and uptake and water use (Zhang and Kirkham, 1994; Munné-Bosch et al., 2001; Shinozaki et al., 2003). Drought resistance mechanisms are complex defence systems that function at the molecular, cellular, biochemical, physiological and morphological levels (Kazan, 2015). The inhibition of rice shoot elongation and growth are part of the drought defence mechanism. Interestingly, shoot inhibition occurs even before the water potential of aerial plants decreases. This phenomenon may occur in response to signals in the root induced by ABA and ethylene. Stomatal closure is another potential defence mechanism that promotes drought tolerance by reducing transpiration-mediated water loss. This mechanism is dependent upon the turgor pressure in guard cells (Fang and Xiong, 2015). Under drought stress, hormonal signals decrease transpiration by regulating the turgor pressure of these cells, thereby optimising gas exchange and water loss. Although ABA is the stress phytohormone that most effectively controls the stomata under drought stress, recent evidence has confirmed a role of the ABA-independent signalling network in stomatal regulation under such conditions (Danquah et al., 2014; Li et al., 2015).

An increased level of the ethylene precursor ACC in rice roots might promote the shoot inhibition phenomenon that occurs under salinity stress (Saab and Sharp, 1989; Gómez-Cadenas et al., 1996). In the presence of a water deficit, ethylene biosynthesis is increased in rice. Expression of the ethylene biosynthesis-related genes ACO and ACS may be altered in response to water deficit (Nakano et al., 2006). As mentioned above, 1-aminocyclopropane-1-carboxylic acid is the ethylene precursor that forms ethylene in a reaction catalysed by ACS (Broekaert et al., 2006). Genes in multiple families, which are regulated in a tissue-dependent or independent manner, encode the ACO and ACS enzymes and are activated in response to environmental factors (Grichko and Glick, 2001). Evidence from molecular and genetic investigations of transgenic rice indicate that overexpression of the AP2/ERF genes in rice enhances the resistance of transgenic plants to drought stress (Pan et al., 2012). TERF1 is an ERF family member that participates in the ethylene response pathways in tomato. Overexpression of TERF1 in rice enhances tolerance to both drought and salinity by promoting the accumulation of proline and decreasing water loss (Gao et al., 2007). Further, the JERF1 tomato gene is induced by ethylene, ABA, NaCl, and jasmonic acid. Overexpression of recombinant JERF1 in transgenic rice has been shown to increase drought, cold and biotic tolerance by binding to the DER and GCC-box (Zhang et al., 2004). Additionally, knockdown of OsDERF1 (class II) promotes the tolerance of transgenic rice during the tillering and seedling stages. The ethylene level has also been reported to be decreased during the seedling stage in transgenic rice via interactions of OsDERF1 with the GCC boxes in the promoters of the ERF repressors OsAP2-39 and OsERF3. Furthermore, the overexpression of OsAP2-39/OsERF3 suppresses ethylene synthesis (Wan et al., 2011). The OsDREB1F gene is activated by both ABA-dependent and independent pathways and by the ICE1 protein in rice plants subjected to drought, salt or cold stress. This gene binds to the CRT/DRE, which induces the expression of genes that contain the CRT/DRE sequence in their promoter regions, including COR15a and rd29A (Wang et al., 2008). The functions of other ERFs in the ethylene network in response to drought stress have not yet been analysed.

10. Ethylene and ERF performance in rice in response to heavy metal stress

Heavy metal ions are natural components of the earth's crust that play pivotal roles in many physiological and biochemical processes (Thao et al., 2015). Trace quantities of many of these ions are needed for growth, metabolism and development. However, excess amounts of these ions leads to toxicity and cellular damage in plants (Avery, 2001; Schützendübel and Polle, 2002; Gaetke and Chow, 2003; Polle and Schützendübel, 2003). Heavy metal toxicity symptoms are caused by the inactivation of biomolecules by either the displacement of vital metal ions or by the blocking of vital functional groups (Goyer, 1997; Thao et al., 2015). Furthermore, ROS production, as well as redox-active heavy metal autoxidation by the Fenton reaction causes cellular injury (Stohs and Bagchi, 1995). It is well known that plants under heavy metal stress synthesize cysteine-rich proteins, including metal-binding peptides, such as metallothioneins and phytochelatins (Clemens, 2001; Jonak et al., 2004). Thus, heavy metals can be detoxified by their sequestration and chelation in vacuoles, and several membrane transport networks play pivotal roles in metal ion tolerance and homeostasis (Clemens, 2001; Cobbett and Goldsbrough, 2002; Hall and Williams, 2003). In crops, convincing evidence indicates that the ethylene, jasmonic acid and salicylic acid levels increase following exposure to heavy metal stress (Cánovas et al., 2004; Maksymiec et al., 2005; Metwally et al., 2005).

Cadmium (Cd) and copper (Cu) are heavy metals with diverse physiochemical functions and properties (Jonak et al., 2004). Copper is a pivotal micronutrient for crop growth and development. This heavy metal is a cofactor for several physiological pathways, including ethylene sensing, respiration, photosynthesis, metabolism, lignification and superoxide scavenging. Nonetheless, excess concentrations of copper are harmful because they induce ROS production by the Fenton reaction and autoxidation (Schützendübel and Polle, 2002; Jonak et al., 2004). As mentioned above, the ERF superfamily has been reported to be involved in the ethylene signalling pathway in plant abiotic stress responses (Nakano et al., 2006). ERF gene induction by Cd in Anemone halleri, Arabidopsis thaliana and Oryza sativa has also been reported (Weber et al., 2006; Thapa et al., 2012). The Cd-induced expression of various ERF genes indicates that the ERF proteins might be specific to diverse genes that are expressed in response to different Cd levels (Nakano et al., 2006; Thapa et al., 2012). It has been demonstrated that DREB is down-regulated in response to heavy metal stress in the ethylene pathway (Nakashima and Yamaguchi-Shinozaki, 2006). Therefore, the down-regulation of these stress-related transcriptional regulators may play key roles in the transcriptional regulation of stress- responsive genes under Cd acclimation in crop roots. These results suggest that the down-regulation of DREBs in plants under heavy metal stress allows for maintenance of the osmotic potential in the cell membrane and the decreased inflow of heavy metal-contaminated water. As a result, the heavy metal concentrations are reduced at the cellular level, and the heavy metals are loaded into transport vesicles to prevent phytotoxic effects. This can provide an initial defence mechanism in plants exposed to heavy metal stress (Nakano et al., 2006; Thapa et al., 2012).

During flooding or waterlogging, the concentration of the heavy metal chromium (Cr) is increased, and this increase is correlated with the soil pH (Zarcinas et al., 2004). Cr(VI) toxicity causes oxidative stress, which is an obstacle to the growth of rice seedlings (Panda, 2007; Zeng et al., 2012). Analysis of rice roots after 1 or 3 h of exposure to Cr(VI) stress has revealed that vesicle trafficking, ethylene signalling, ethylene biosynthesis and ROS modulation are related to the chromium signalling pathway

Pathogens

↓

EIN3/EIL1

↓

ERF1 and
other ERFs

↓

PRs (*Pdf1.2* and *PR-4*)

↓

Ethylene-Dependent
Diseases Resistance
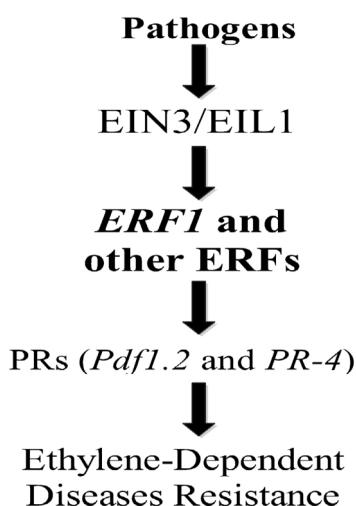
Fig. 4. Schematic diagram of ethylene-dependent pathway activity in response to pathogens in rice.

(Huang et al., 2014; Trinh et al., 2014). The up-regulation of ACO4, ACO5, ACS1 and ASC2 in rice under chromium stress indicates that ethylene synthesis is part of the chromium pathway (Rzewuski and Sauter, 2008; Trinh et al., 2014). As mentioned above, ACS1 expression is induced by H_2O_2, ethylene, anoxia, hypoxia and infection by the fungus *Magnaporthe grisea* (Zarembinski and Theologis, 1997; Iwai et al., 2006; Steffens and Sauter, 2009; Steffens, 2015). In rice, various genes in the AP2/ERF family have been shown to be up-regulated in response to chromium stress, and they may also play roles in the ethylene synthesis networks. These genes include *ERF120* (subgroup Ib), *ERF077* (subgroup VIIIa), *ERF068* and *ERF067* (subgroup VIIa) (Nakano et al., 2006; Trinh et al., 2014; Steffens, 2015). However, little is known regarding the involvement of ERF expression in the mechanism of action of ethylene in the response to heavy metal stress in plants.

11. Coordinated response of ethylene and ERF to biotic stress in rice

Ethylene biosynthesis is one of the immune responses of crops to pathogen attack, and it is associated with the induction of defence reactions (Mattoo and Suttle, 1991; Gamalero and Glick, 2015). Generally speaking, it is assumed that ethylene biosynthesis under biotic stress contributes to the alleviation of adverse effects, while some crop pathogenic bacteria and fungi biosynthesise ethylene as a virulence mechanism to improve their abilities to colonize crop tissues (Chagué et al., 2006; Das et al., 2015). Relevant studies have revealed that ET biosynthesis in response to pathogenic attack promotes disease development rather than

alleviating it (Tzeng and De Vay, 1985). A number of studies have shown that the treatment of plants with ethylene increases disease development by accelerating senescence or ripening. However, another previous study has demonstrated that ethylene application before pathogen infection has no impact on or reduces disease development, whereas ET treatment after photogene induction accelerates disease development. Therefore, the timing of plant exposure to ethylene can determine whether resistance is reduced or stimulated (Abeles et al., 1992).

Among the regulators of ethylene, the AP2/ERF factors have a regulatory role in the expression of pathogenesis-related (PR) genes. ERF family members bind to the GCC-box in the promoter of the ethylene-inducible *PRB-1b* gene. Upon binding of the ERFs to this GCC-box, PR gene expression is rapidly induced following pathogen infection (Eyal et al., 1993). *ERF1* acts downstream of EIN3/EIL1 and is rapidly induced by both jasmonic acid and ethylene. *ERF1* activates the expression of defence-related genes, including *Pdf1.2* and *PR-4*, as well as jasmonic acid-inducible genes, in response to bacterial and fungal infections (Fig. 4) (Berrocal Lobo et al., 2002; Van Loon et al., 2006). The expression of *OsERF1* and *OsACS2* in the presence or absence of *Xanthomonas oryzae pv. oryzae (Xoo)* has been shown to be significantly suppressed in *OsEDR1-KO* rice (Shen et al., 2011). In addition, the overexpression of *OsERF1* in *Arabidopsis* has been demonstrated to regulate two ethylene-responsive genes, namely b-chitinase and *PDF1.2*, as well as the ethylene-hypersensitive phenotypes (Hu et al., 2008; Yang et al., 2015). In accord with these findings, Iwai et al. (2006) and Hu et al. (2008) have demonstrated that *OsACS2* may be involved in the ethylene synthesis pathway and that *OsERF1* functions in the ethylene response network.

The general findings obtained using rice genome microarrays have indicated that *OsBIERFs*, *OsERF1* and *Pti4* are transcriptionally regulated by jasmonic acid, ethylene and pathogens. As shown in Table 2, the *OsBIERFs* are classified according to the *Arabidopsis* genes (Gutterson and Reuber, 2004). Classification of the rice and *Arabidopsis* ERF genes indicates that they might have similar responses to ethylene, jasmonic acid and pathogens. On the other hand, *OsEBP2*, which is orthologous to *OsBIERF1*, is expressed in response to ethephon (a plant growth regulator that converts ethylene in plants) (Schaller and Voesenek, 2015), ABA and MeJA. The induction of *OsEBP2* expression occurs during the initial period (4–8 h) after treatment with ethylene, jasmonic acid or ABA. Based on the identified *cis*-elements in the promoter, *OsEBP2* may be induced in rice as a defence response to infection by blast fungus (Lin et al., 2007). Further, *OsEREBP1*, which binds to the ethylene-responsive element (ERF) GAGCCGCC, has been reported to be expressed in *Magnaporthe grisea* (Han et al., 2004). *OsBIERF3* is another ethylene response element-binding factor in rice whose expression is induced by various chemicals produced during biotic stress responses, such as those generated in response to blast fungus infection. In addition, overexpression of this gene in tobacco has been reported to enhance the resistance of transgenic plants to disease (Cao et al., 2006).

Table 2
Classification of *OsBIERFs* based on the ERF cluster.

Gene	ERF class	Related gene in the class	Function	References
OsBIERF1/ OsBIERF4	IV	–	Unknown function of N-terminal MCGGAII/L. Unlikely to be required for binding to the GCC box or nuclear localisation	Tournier et al. (2003)
OsBIERF2	II	*NtERF3* (tobacco), *AtERF3/AtERF4* (*Arabidopsis*)	Transcription active repressors	Fujimoto et al. (2000), Ohta et al. (2000) and Ohta et al. (2001)
OsBIERF3	I	*AtERF1/AtERF2* (*Arabidopsis*), *NtERF1/ NtERF2* (tobacco) and *Pti4* (tomato)	Transcriptional activator	Zhou et al. (1997), Solano et al. (1998), Fujimoto et al. (2000) and Ohta et al. (2000)

12. Future perspectives

Ethylene interacts with AP2/ERF family members under stress conditions in rice. To date, several AP2/ERF genes that are expressed in response to adverse conditions have been identified in association with molecular signalling pathways. An understanding of the molecular and genetic pathways involving the AP2/ERF genes and their interactions with ethylene may assist researchers in developing plants that are tolerant to adverse environmental conditions. This overview of the influences of the AP2/ERF family genes on ethylene performance has revealed that improvements in the abilities of crops to adapt to adverse conditions can be achieved using this network. Transcription factor proteins play pivotal roles in the regulation of physiological, morphological and biological pathways in plants in response to environmental conditions (Rashid et al., 2012). Together with plant physiological approaches, conventional plant breeding, genetic (Sahebi et al., 2015), genetic engineering (Abiri et al., 2015) and biochemical approaches used to investigate plant responses to adverse conditions have recently begun to increase plant and fruit yields worldwide (Gao et al., 2007; Nejat et al., 2015).

Conflicts of interest statement

The authors declare that they have no conflicts of interest.

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