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Review

The significance and functions of ethylene in flooding stress tolerance in plants

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ABSTRACT

Climate change has increased the global environmental risks, especially the impacts of abiotic stresses on agriculture productivity. Among the abiotic stresses aggravated by climate change, flooding (complete submergence, stagnant flooding, soil waterlogging) has been identified as a major stress for plant growth and food production worldwide. Improving crop plants adaptation to flooding conditions is important to cope with increasing incidences and intensity of flooding, which could potentially be accomplished through manipulating adaptive physiological and molecular processes. Ethylene is a key plant hormone in plant adaptation to flooding, modulating signaling, and metabolic responses. Significant progress was made in understanding the basic physiological and molecular mechanisms associated with ethylene-mediated plant responses to flooding stress, though our knowledge in this field is still far from complete. This review provided (a) an overview of ethylene biosynthesis, signaling and its perception under flood condition in plants, with emphasis on rice; (b) assess the ethylene functions under flooding stress based on available evidences; (c) cross-talks of ethylene with other phytohormones and signaling molecules associated with ethylene-induced flooding responses; and (d) elucidate the role of ethylene mediated tolerance pathways with an aim of developing flood tolerant plants. The review represents a step forward to develop flood resilient crop plants by exploiting the knowledge of ethylene biology and functions.

1. Introduction

In the present scenario of climate change, flooding is a major agricultural threat for food production and economic growth worldwide (Ismail, 2013; Tamang and Fukao, 2015; Mondal et al., 2020). Complete submergence reduces diffusion of oxygen (O_2) and carbon dioxide (CO_2) by about 10,000-fold, increases ethylene synthesis and entrapment in plant tissue and restricts light availability (Fukao and Bailey-Serres, 2008a). In fact, submergence stress influences almost all aspect of plant growth and development, from seed germination to maturity (Ismail, 2013). Under partial submergence, some portions of the plant remain above the water surface resulting in low O_2 levels near root-shoot junctions due to decreased O_2fluxes from shoots to roots (Van Bodegom et al., 2008). During floods, whether partial or complete, gas exchange is severely restricted between the plant and its environment and when O_2 becomes limiting plants suffer from severe O_2 deprivation

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Abbreviations: ABA, abscisic acid; ACC, 1-Aminocyclopropane-1-carboxylic acid; ACO, 1-aminocyclopropane-1-carboxylic acid oxidase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; AP2, apetala 2-like proteins; AVG, aminoethoxyvinylglycine; BR, brassinosteroid; EREBP, ethylene-responsive element binding proteins; ERF, ethylene response factor; ERFVII, ethylene response factor (group VII); ETRs, ethylene receptors; GA, gibberellic acid; JA, jasmonic acid; *LGF1*, *Leaf Gas Film 1*; LOES, low-O_2 escape syndrome; LOQS, low-O_2 quiescence syndrome; 1-MCP, 1-methylcyclopropene; MPK3, MITOGEN ACTIVATED PROTEIN KINASE 3; NADPH, nicotinamide adenine dinucleotide phosphate; NO, nitric oxide; NPA, N-1-naphthylphthalamic acid; PB, paclobutrazol; PCD, programmed cell death; PCO, plant cysteine oxidases; *PGB1*, *phytoglobin1*; *QTL*, *quantitative trait loci*; *RBOHS*, *respiratory burst oxidase homologs*; ROS, reactive oxygen species; ROAD, rice oligonucleotide array database; SA, salicylic acid; *SK1/2*, *SNORKEL1/ SNORKEL2*; *SLR1/2*, *SLENDER RICE-1/ SLENDER RICE-2*; *Sub1*, *submergence1*; XET, xyloglucan endo-transglycosylase; ZR, trans-zeatin-riboside

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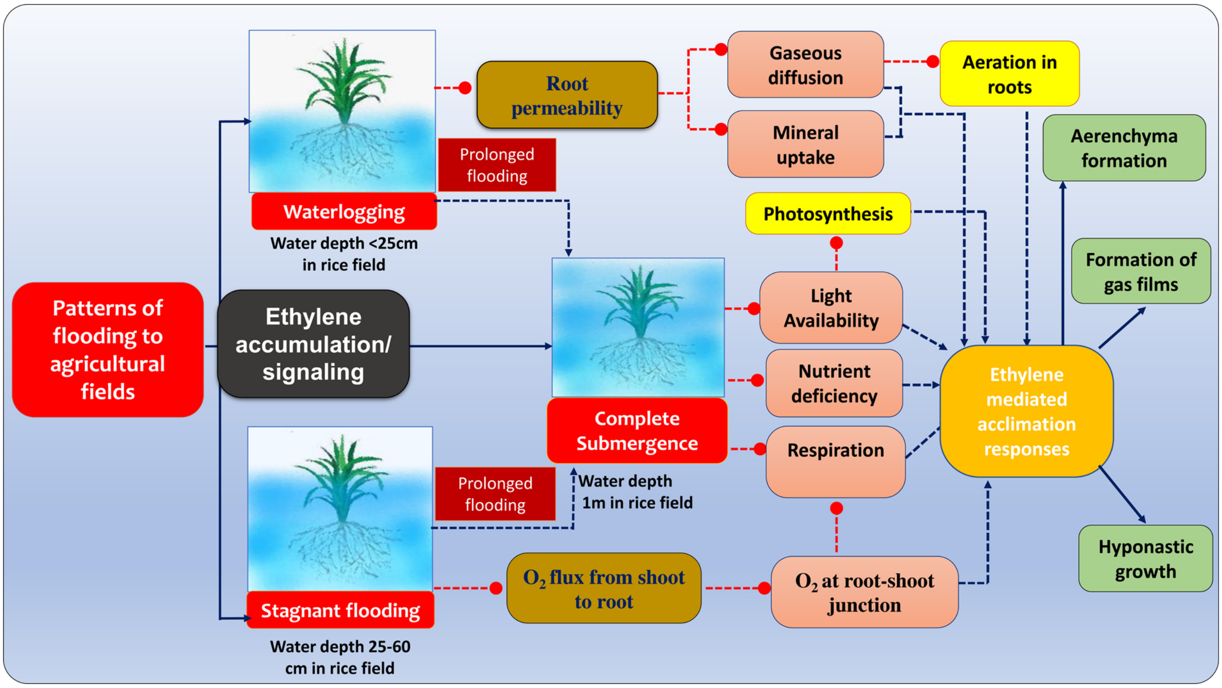

Fig. 1. Different types of flooding, their effects on plants and adaptive mechanisms. Environmental conditions such disturbances in weather patterns, excess irrigation without proper drainage and increasing sea level might lead to three different types of flooding, namely complete submergence, stagnant flooding and soil waterlogging. Each flood type has its own specific effect on plants, however prolonged waterlogging and stagnant floods triggers different responses based on plant species and adaptation to aquatic conditions. Floods that affect plant growth triggers ethylene regulated acclimation responses, including aerenchyma formation and formation and retention of gas films. Red dotted lines with round heads indicate the negative effects of flooding on plant processes. Blue dotted lines with arrow heads indicate ethylene mediated acclimation responses, solid blue lines with arrow heads are examples of acclimation responses regulated by ethylene (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(hypoxia), which affects two vital plant processes: photosynthesis and respiration, resulting in energy crisis (Van Bodegom et al., 2008; Perata, 2019). As a consequence, in any type of flooding, persistence of stress would finally lead to similar chain of effects such as reduction in root permeability, mineral uptake, photosynthesis, stomatal conductance, modulation of hormonal homeostasis, and development of aerenchyma, and increase in reactive oxygen species (ROS), causing premature plant mortality (Voesenek et al., 2006; Nishiuchi et al., 2012; Wu and Yang, 2016). The plasticity of plants allows adaptation to adverse environments transiently or permanently through modulating their physiological, biochemical, and molecular processes. Plants undergo several different adaptive responses to improve their surviving ability under flooding conditions such as aerenchyma formation in roots to facilitate gaseous exchange during anaerobic conditions (Armstrong, 1979). However, partial submergence triggers additional adaptive strategies such as hyponastic growth and fast elongation of aerial organs to maintain adequate aeration (Cox et al., 2003). Plants under complete submergence primarily undergo induction of aeration, maintenance of ROS formation induced by re-oxygenation and recovering reproduction viability under stress (Voesenek and Bailey-Serres, 2015; Fig. 1). A summary of the experimental manipulation of ethylene and the ethylene-induced responses in flooded plants reflected its involvement in a wide range of plant functions (Table 1).

Phytohormones play an essential role in a wide range of physiological and developmental processes in plants and regulate plant-signaling networks as they induce wide range of responses against abiotic stresses (Khan et al., 2012; Kazan, 2015; Thao et al., 2015). Ethylene is a gaseous phytohormone and has significant role in plant responses to external stimuli to improve adaptation and productivity of agricultural systems. It has a wide range of effects on plant growth and development; and regulates several processes including seed germination, sex determination, leaf, stem, and root growth, fruit ripening, abscission of plant organs, and senescence (Iqbal et al., 2017). In addition, ethylene plays a pivotal role in plant stress responses when plants are subjected to abiotic stresses (Kazan, 2015; Thao et al., 2015). It has been well documented that ethylene accumulation triggers an array of stress adaptative responses in flooded plants that are crucial for inducing tolerance and sustaining survival. It mediates the growth of shoots towards the water surface that facilitates gas exchange with the atmosphere; the development of adventitious roots; and maintenance of basic metabolism required for surviving submergence (Fukao et al., 2006; Fukao and Bailey-Serres, 2008a; Steffens and Rasmussen, 2016; Alpuerto et al., 2016; Yamauchi et al., 2014, 2017; Hartman et al., 2019, 2020; Wang et al., 2020). Additionally, ethylene accumulation is a key signal associated with flooding that decreases O_2 availability. The low O_2 availability response is largely under the control of the ethylene response factor (ERF) group VII (ERFVII) transcription factor family mediated via the N-end rule pathway of targeted proteolysis (Gibbs et al., 2011; Licausi et al., 2011; Giuntoli and Perata, 2017). Under normoxia, ERF VII N-terminal cysteine residue is subjected to O_2-dependent degradation through the N-end rule pathway by plant cysteine oxidases (PCO; Bailey-Serres et al., 2012). While under hypoxia, the PCO activity is limited slowing the degradation of ERFVIIs that accumulates, switching hypoxia-responsive gene transcription (Gibbs et al., 2011; Licausi et al., 2011). Hartman et al. (2019) also revealed a link between ethylene signaling and O_2 sensing machinery for the regulation of flooding survival. Flood-adapted plants evolved two different growth-related flooding survival strategies, the low-O_2 escape syndrome (LOES) and low-O_2 quiescence syndrome (LOQS) (Voesenek and Bailey-Serres, 2015) and the entrapped ethylene is the primary regulator for both of these contrasting strategies (Bailey-Serres et al., 2010; Sasidharan and Voesenek, 2015).

There are also evidences where ethylene plays a negative role in surviving flooding stress (Vidoz et al., 2016; Mira et al., 2016), while in other cases it does not play any apparent role (Müller, et al., 2019), and in others, it was selected against during evolution for adaptation to

Table 1
Overview of exogenous or endogenous effects of ethylene on plant responses under flooding. The experiments and results reported exemplify the main results in context of this review.

Plant species	Concentration of ethylene	Parameter (s) studied	Nature of flood	Effect on plant	References
Oryza sativa	100 mgL^{-1} ethephon	Expression of xyloglucan endotransglycosylase (*XET*) gene	Waterlogging/ anaerobic flooding for 48 h	Aerenchyma development in root	Yu et al. (2009)
Oryzasativa	100 mgL^{-1} ethephon	Decreased SOD activity	Waterlogging/ anaerobic flooding for 48 h	Accumulation of reactive oxygen species and other free radicals in root cells.	Yu et al. (2009)
Oryza sativa	10 μL L^{-1} ethylene gas	Plant height and thousand-grain weight	Complete submergence for 4d	Ethylene treatment enhanced coleoptile elongation, mesocotyl growth, increased plant height, grain length and weight.	Ma et al. (2013)
Oryza grandiglumis	10 μL L^{-1}	Internode elongation	Partial submergence for 3d	Induced ethylene accumulation but did not affect internode elongation	Okishio et al. (2014)
Rumex pahstris Sm.	1.8 and 9.1 μL L^{-1} Ethylene nutrient solution	Adventitious root	Waterlogging/ anerobic flooding for 2d	Increased the number of adventitious roots	Visser et al. (1996)
Dendranthema zawadskii	340 μL ethylene 0.05 − 0.25 μl g^{-1} h^{-1}	Alcohol dehydrogenase and pyruvate decarboxylase gene expression	Waterlogging for 24h	In tolerant species, ethylene appeared to signal an acceleration and induced programmed cell death and aerenchyma formation and alleviate ethanolic fermentation.	Yin et al. (2013)
Oryza sativa	1 or 100 μL L^{-1} ethylene gas for 6 h.	Chlorophyll, carbohydrates, ethanol, pyruvate decarboxylase and alcohol dehydrogenase	Complete submergence for 14 days	Suggestion of a model for the ethylene- and GA- regulation of genes involved in the acclimation to submergence.	Fukao et al. (2006).
Ranunculus sceleratus	50 nL mL^{-1} ethylene	Plant growth, petiole elongation	Complete submergence for 3 days	Increase auxin (IAA) transport through petiole sections within 1 h of treatment.	Musgrave and Walters (1973).
Oryza sativa	50 μL L^{-1} ethylene or 50 μM ACC	Plant growth, ABA; gene expression of *OsABA8ox1*	Complete submergence for 8 days	Results indicate that the ABA decline is partially mediated by ethylene.	Saika et al. (2007)
Rumex palustris	5 μL L^{-1} ethylene for 1 − 4 h	Plant growth, ABA, genes involved in ABA biosynthesis, GA.	Complete submergence for 19 days	ABA is an inhibitor of petiole elongation induced by ethylene.	Benschop et al. (2005)
Rumex palustris	5 μL L^{-1} ethylene	Apoplastic pH measurement, Expansin activity, petiole elongation	Complete submergence for 10 h	Ethylene induced fast net H + extrusion, leading to apoplastic acidification and up-regulated expansin genes.	Vreeburg et al. (2005)
Rumex palustris	5 μL L^{-1} ethylene	Hyponastic growth, hormonal changes and expansins	Partial submergence for 16 h	The hormones regulated the hyponastic growth of petiole and no differential expression of expansins across the petiole base was found.	Cox et al. (2004)
Oryza sativa	1 or 100 μL L^{-1} ethylene for 6 h.	Shoot elongation, hormone changes,	Complete submergence for 14 days	Sub1A reduces ethylene-promoted GA response during submergence and induces GA signaling repressors SLR1 and SLRL1.	Fukao and Bailey-Serres (2008b)
Rumex palustris and R. acetosa	5 μL L^{-1} ethylene	Petiole growth and gibberellin levels	Complete submergence for 48 h	Submergence and ethylene induce tissue GA sensitivity in *R. palustris*, in *R. acetosa*ethylene de-sensitized petioles to GA$_3$.	Rijnders et al.(1997)
Oryza sativa	10 μL L^{-1} ethylene for 3 h	Gene expression of ethylene receptors	Complete submergence for 12 weeks	Ethylene induces receptors homologous to Arabidopsis thaliana ETR2 and EIN4 in rice.	Watanabe et al. (2004)
Zea mays	5 μL L^{-1} ethylene	Plant growth and root development.	Waterlogging/ anaerobic flooding for 7d	Induced adventitious roots and aerenchyma formation	Drew et al. (1979)
Oryza sativa	10 mM ACC	Cell vitality	Stagnant flooding/ partial submergence for up to 18 h	Ethylene induced cell death and adventitious roots development	Mergemann and Sauter (2000)
Oryza sativa	1 − 4 nmol g^{-1} FW of ethylene	Internode elongation	Stagnant flooding/ partial submergence for 7 days	Internode had a much higher ethylene in stressed plants and stimulates growth in submerged.	Metraux and Kende (1983)
Oryza sativa	0 − 150 μ Ethephon	Cell death, petiole elongation, roots development	Complete submergence for 10 − 11 weeks.	Ethylene and GA have synergistic effect. ABA delays the effect of ethylene.	Steffens and Sauter (2005)

aquatic conditions (Golicz et al., 2015). Vidoz et al. (2016) analyzed the *aer* tomato mutant (resembles the wild type but with numerous quiescent adventitious root primordia formed along the stem) behavior to flooding, analyzing several ethylene-induced responses such as epinasty, hypertrophy, aerenchyma and apical hook formation. They found that the partial ethylene insensitivity found in *aer*, together with the fast development of a new adventitious root system, favors tomato plant adaptation to flooding (Vidoz et al., 2016). In watercress *(Nasturtium officinale*), a non-rosette growing Brassicaceae species, Müller et al. (2019), elucidated the submergence-induced internode elongation response at molecular and physiological level. Using ethylene function modulators (ethylene perception inhibitor, 1-methylcyclopropene (1-MCP) and ethylene biosynthesis inhibitor, aminoethoxyvinylglycine (AVG), the authors observed that underwater stem elongation was partially blocked, with no effect on petiole growth suppression. Their data suggests that the watercress underwater elongation cannot be fully attributed to ethylene, since the inhibition of ethylene signaling or biosynthesis only plays a minor role in the submergence-induced growth responses. Interestingly, several aquatic species that remain fully submerged throughout their life cycle has lost the ability to synthesize ethylene (Golicz et al., 2015; Summers et al., 1996). Voesenek et al. (2015) suggested the lack of ethylene biosynthesis and/or signaling was probably selected against during the transition of some angiosperm plants from a terrestrial to an aquatic lifestyle. In fact, increasing ethylene in these permanently submerged aquatic plants could severely affect plant development as observed in a constitutive ethylene signaling mutants of *Arabidopsis thaliana* (Kieber et al., 1993; Voesenek et al., 2015).

These studies clearly showed that the responses that ethylene mediates under flooding are species specific. However, in some plant species like rice, where ethylene mediates some of the major flooding responses, exploitation of these responses to improve flooding tolerance is of paramount importance. This review is an attempt to advance our understanding about the significance of ethylene in improving flooding stress tolerance in plants. It elucidates the common mechanisms mediated ethylene under different types of flooding and the strategies adopted for tolerate by different plant species, with main emphasis on rice as an important crop in humid tropics and other areas affected by excessive wetting.

2. Ethylene biosynthesis and signaling under flooding stress

The mechanism underlying ethylene biosynthesis is quite different under stress and control conditions. Abiotic stresses such as chilling (Catala et al., 2014), salt (Shen et al., 2014), drought (Daszkowska-Golec and Szarejko, 2013), heat (Clarke et al., 2009), flooding (Hattori et al., 2009; Pen˜a-Castro et al., 2011), heavy metals (Thao et al., 2015) and photo-oxidative stress (Satoh et al., 2013) induces its biosynthesis, reflected as burst in ethylene concentration (Stearns and Glick, 2003). Complete submergence accelerates the production and accumulation of ethylene in most plant species (Voesenek et al., 2003; Jackson, 2008; Alpuerto et al., 2016). In contrast to other stresses, where gas diffusion is not impaired, gas exchange is severely restricted between the plant and its environment under flooding. Submergence promotes biosynthesis of ethylene, which is entrapped in plant tissues, rapidly reaching response-saturating levels within $1-2$ hours (Banga et al., 1996; Voesenek and Sasidharan, 2013). This will then initiate flood-adaptive responses, which allow a range of species to inhabit and survive temporarily flooded habitats. Understanding ethylene dynamics–biosynthesis, signaling and perception in flood tolerant plants could therefore be useful for enhancing tolerance of important food crops.

Among the submergence tolerant species, rice (*Oryza sativa*) is the most studied food crop for its agricultural and economic importance. Here, we evaluated the involvement of ethylene biosynthetic and signaling genes in rice responses to submergence at the transcription level using bioinformatics tools. Firstly, ethylene related genes of rice were selected from Rap-db (http://rapdb.dna.affrc.go.jp/) and Uniprot (www.uniprot.org/) databases. A total of 395 genes were obtained (Supplementary Table S1) and further classified into ethylene biosynthetic genes, ethylene sensing genes, ethylene signaling genes and ethylene-induced responses genes (Supplementary Table S2, S3, S4 and S5, respectively).

In silico analysis of submergence stress libraries was initially performed using Rice Oligonucleotide Array Database (ROAD) (www.ricearray.org/) (Cao et al., 2012), followed by a microarray study using aerial tissues of the submergence tolerant M202-Sub1 and the intolerant M202 rice varieties (Mustroph et al., 2010). Rice accessions that lack the *SUB1* gene *SUB1A* (e.g. M202) usually die within 7 d of complete submergence. By contrast, genotypes containing *SUB1A* (e.g. M202-*Sub1*) can endure submergence stress for over 14 days (Fukao et al., 2006; Xu et al., 2006; Ismail et al., 2013; Alpuerto et al., 2016). To gain insights into submergence-induced expression profile of ethylene-related genes between these contrasting genotypes, the publicly available microarray data on the Affymetrix Rice Genome Array was analyzed using Genevestigator (Hruz et al., 2008). The experiment assessed transcriptional regulation in seedlings submerged for 24 h (S) *vs* non-submerged shoots (UT) as control. The fold change values were hierarchically clustered by gene values using Euclidean distances. This meta-profiling showed that the ethylene biosynthetic pathway is regulated similarly in the tolerant and intolerant accessions under flooding stress (Fig. 2A). The 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) genes *ACO8* and *ACO3* were strongly induced in submerged shoots, whereas *ACO1* was negatively regulated. However, the comparison of the tolerant (M202-*Sub1*) and the intolerant (M202) accessions showed that evolution of ethylene was significantly higher in the genotypes, which were submergence intolerant compared to the tolerant one (Bailey-Serres et al., 2010). Probably, this process is regulated transcriptionally by 1-aminocyclopropane-1-carboxylic acid synthase (*ACS*) gene *ACS2* that was repressed in the tolerant genotype (Fig. 2A). In rice grown under hypoxic conditions, two *ACS* genes, *ACS1* and *ACS5* are highly expressed (van der Straeten et al., 2001) and are differentially expressed in the tissues under submergence. The ACS1 transcripts were localized in internodes, in particular in the cell elongation zone (Zarembinski and Theologis, 1997), and were induced after 6 h of submergence. The *ACS5* transcripts expression is in the zone where extensive cell division and elongation take place such as in the vascular bundles of leaf sheaths and young stems (Zhou et al., 2002; Fukao and Bailey-Serres, 2008a).

Alteration in cell and organ structures facilitates enhanced gaseous exchanges during submergence stress (Bailey-Serres and Voesenek, 2008). Increased ethylene concentration in submerged tissues triggers a wide range of acclimation responses, such as formation of adventitious roots, shoot elongation, carbohydrate consumption, aerenchyma development, and ethanolic fermentation (Bailey-Serres and Voesenek, 2008; Jackson, 2008; Drew, 1997; Fukao et al., 2006). During submergence, the levels of *ACS1* mRNA increases only in internodes, which contains cell elongation zone, while other parts of the same stem, including the cell differentiation zone, intercalary meristem and nodes, had lower levels of *ACS1* mRNA during submergence than in air (Zarembinski and Theologis, 1997). Similar increase was observed in *ACS5* mRNA expression in vascular bundles of young stems and leaf sheaths where cells vigorously divide and elongate during the stress (Zhou et al., 2002). The study also suggested that, *ACS5* and *ACS1* together aid in ethylene biosynthesis under prolong submergence conditions, and trigger internode elongation and vigorous cell division and elongation in vascular bundles of young stems.

The last enzyme involved in the ethylene biosynthesis is the ACO and its activity decreases when $O_2$is limited, since ACO requires O_2 to catalyze the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene. In rice, when $O_2$is limiting, the transcripts of *ACO1* accumulate in the elongation zones of nodes and internodes (Mekhedov and Kende, 1996). The induction of *ACO1* was recorded after 4 h of

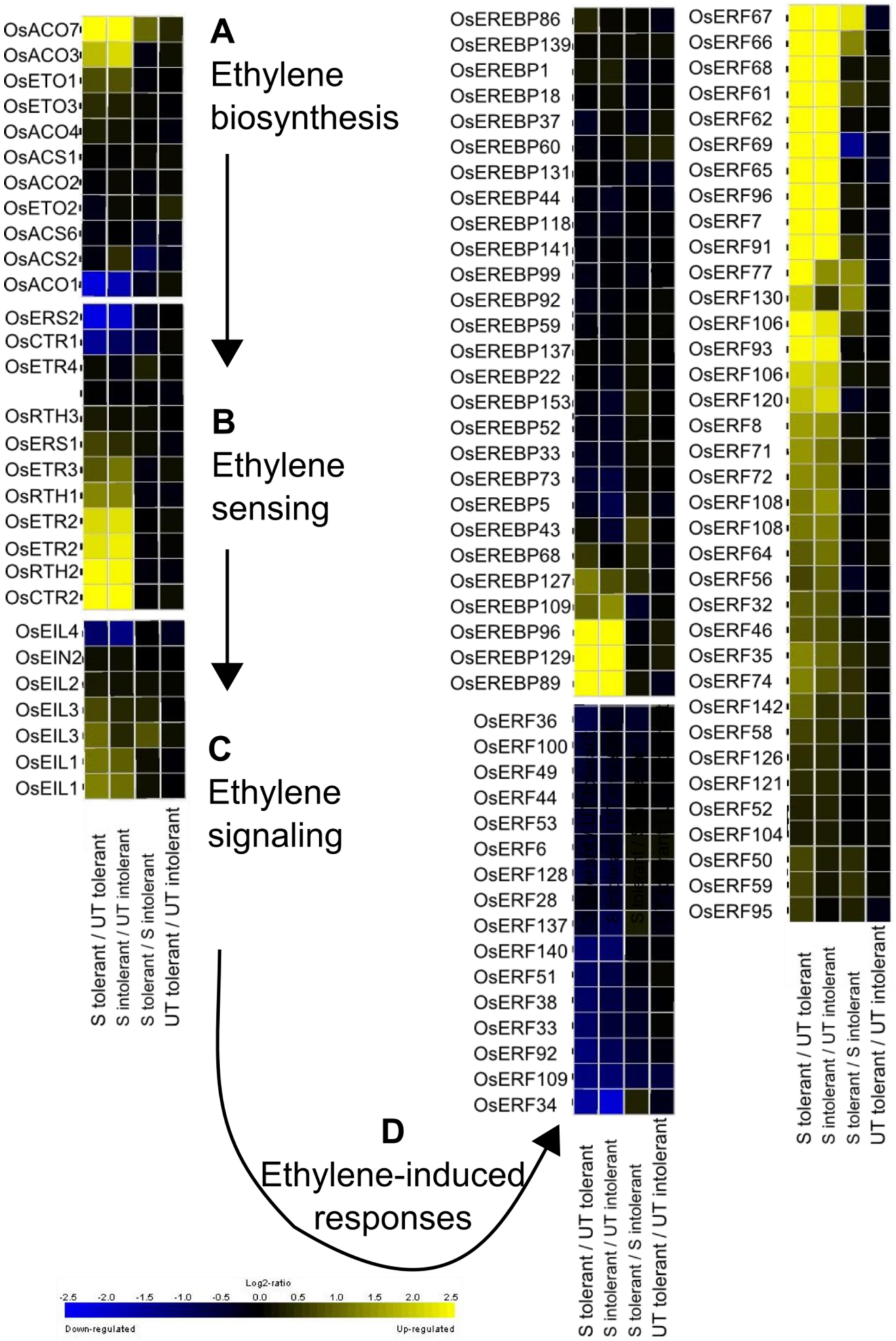

Fig. 2. Meta profiling of ethylene genes regulated by submergence in rice (*O. sativa*). The expression profiles of four ethylene gene lists (Supplementary Table S1-5) following submergence were analyzed using the similarity search tool: ethylene biosynthesis (A); ethylene sensing (B); ethylene signaling (C); and ethylene-induced responses (D). The data consist of four ethylene-related genes represented in the publicly available Affymetrix Rice Genome Array obtained using the Genevestigator toolbox. Blue and yellow colors, respectively, indicate down- and up-regulation; black color indicates no change in expression. The values indicate the fold-change in expression under submergence (S) and untreated shoot (UT) for two rice ecotypes (M2O2-*Sub1*, a tolerant genotype and M2O2, intolerant) contrasting in submergence tolerance (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

submergence (Mekhedov and Kende, 1996) and was maintained for 24 h. Recent studies demonstrated that *OsACO5* was highly expressed in rice under normoxic conditions, suggesting that this gene is mainly involved in aerenchyma formation in aerated roots of rice (Yamauchi et al., 2016). The expression of *ACO1* mediates ethylene accumulation after the initiation of aerenchyma, while *ACO5* is necessary to maintain ethylene synthesis in roots (Yamauchi et al., 2016). The down-regulation of *OsACO1* (by over 5fold) in the tolerant M2O2-*Sub1* might be related to the submergence responses mediated by ethylene, such as shoot elongation and repression of carbohydrate consumption (Yamauchi et al., 2016). Pathways of ethylene signaling in rice are not yet completely elucidated. The ethylene receptors (ETRs), in rice are *OsERS1*, *OsERS2*, *OsETR2*, *OsETR3* and *OsETR4* (Fig. 2B). Under submergence conditions, *OsETR2* is highly expressed in the internodes and is also induced by ethylene (Watanabe et al., 2004). Overexpression of *OsETR2* reduced ethylene concentration and conversely, *OsETR2* knockout plants showed enhanced ethylene sensitivity (Wuriyanghan et al., 2009). Thus, their role ethylene signaling in rice is still not clear. Other components that constitute ethylene signaling cascade isolated so far are ethylene insensitive, such as *OsEIN2* and *OsEIN3/EIN3* like (*OsEILs*) (Rzewuski and Sauter, 2008; Fig. 2C). Upon plant submergence *EIN3EIL* transcription factors (*EIL1* in Rice) are rapidly induced by ethylene at the protein levels and are essential for mediating the downstream ethylene signaling before detrimental effects (hypoxia) occur (Sasidharan et al., 2018). Recent evidence suggested that early ethylene signaling activation (within 1 h) through the prompt stabilization of EIN3 represents the very rapidly perceived flooding signal that is quickly saturated and switched on. For example, EIN3 directly targets and regulates downstream transcription factors that are essential/crucial for submergence-induced underwater hypocotyl elongation (Xie et al., 2015), to enhance hypoxia tolerance in Arabidopsis root tips (Hartman et al., 2019) and for hypoxia tolerance through adaptive remodeling of lipid metabolism (Wang et al., 2020). *In-silico* analysis revealed that submergence activates ethylene signaling through the slight down-regulation of *CTR1* and up-regulation of *EIN3*-like genes (designated *OsEIL1*-4) (Fig. 2B; C). Mao et al. (2006) reported that *OsEIL1* is involved in ethylene signal transduction pathway and positively regulates ethylene response in rice. On the other hand, *OsEIL3* that was slightly upregulated in the tolerant variety was previously reported to have less effect on ethylene response in etiolated seedlings (Yang et al., 2015). The gene sets included in Fig. 2D belong to the B-2 subgroup of the ERFs/ethylene-responsive element binding proteins (EREBPs)/apetala 2-like proteins (AP2). This TF family functions in signaling processes and in environmental stress responses (Vogel et al., 2012) and specifically involved in the mechanisms of submergence tolerance in rice (Fukao et al., 2006; Xu et al., 2006). As per the preliminary data in the rice microarray experiment reported here, rice group VII *ERFs OsERF67, OsERF66, OsERF68, OsERF61*, and *OsERF62, OsERF69, OsERF65, OsERF96, OsERF7,*and*OsERF91* were all induced by more than 10-fold in response to submergence in both rice varieties. The *OsEREBP89*, *OsEREBP129* and *OsEREBP96* genes were strongly upregulated by submergence (Fig. 2C). *OsEREBP*-89 has been shown to be induced by ethylene, 2,4-D, and NaCl in roots of rice (Yang et al., 2002) and its expression was promoted in *OsEIL1*-overexpressing plants (Mao et al., 2006). The *OsEREBP129* and *OsEREBP96* transcription factors (TFs) are RAV TFs. The RAV subfamily is relatively small, with two domains, AP2 domain and B3 domain, and there are five RAV genes in the rice genome (*OsRAVs*) (Sharoni et al., 2011). RAV genes are mainly involved in the control of developmental processes including brassinosteroid (BR) responses, flowering time and leaf senescence (Swaminathan et al., 2008; Woo et al., 2010; Matías-Hernández et al., 2014). Recently, some RAV TFs were reported to be likely involved in plant abiotic stress responses such as cold, drought and salinity (Yamasaki et al., 2004; Li et al., 2015). In a study investigating the molecular responses to waterlogging in *Jatropha curcas* (Jatropha) transcriptional regulation of RAV genes was reported (Juntawong et al., 2014). Despite the strong induction of these TFs under submergence as shown in Fig. 2C (over 15-fold) in both rice varieties, there is no direct implication of RAV-type members in submergence tolerance in rice. Therefore, modulation of ethylene biosynthesis under flooding conditions could provide possible targets for developing flood-tolerant cultivars in the future.

3. Involvement of ethylene in ROS-signaling and modulation of antioxidant system under flooding stress

Production of excess ROS in response to abiotic stresses is a common metabolic phenomenon. Under submergence, it has been noted that limitation in gas diffusion resulted in O_2shortage and accumulation of ethylene in submerged tissues. Importance of ROS during hypoxia signaling under complete submergence conditions (Baxter et al., 2014; Fukao et al., 2011; Liu et al., 2015) is exemplified through several investigations of which RESPIRATORY BURST OXIDASE HOMOLOGs *(Rbohs)* forms an important part. During submergence stress, gas exchange is disrupted and O_2 deficiency results in an oxidative burst derived by nicotinamide adenine dinucleotide phosphate (NADPH) oxidase, which certainly results in post-translational activation of diverse TFs. Later, calcium signaling involving influx of extracellular calcium stimulates a signaling cascade, which involves the activation of NADPH oxidases, called RBOHs. A recent investigation reported that expression of *RBOHH*, an isoform of RBOHs is regulated by ethylene signaling, while examining the effect of ethylene on the RBOH-mediated ROS production during induction of aerenchyma formation in rice roots (Yamauchi et al., 2017). In this study, 10-D-old seedlings of rice were grown in sufficient O_2 and were then treated with ethylene inhibitor 1-MCP (2 ppm) under stagnant flooding (partial flooding), which led to suppression in aerenchyma formation at 48 h of stagnant condition, 10 mm from the tips of adventitious roots (Yamauchi et al., 2017). In this study, the expression of *ADH2* and *RBOHH* was also suppressed by ethylene inhibitor 1-MCP indicating the correlation of RBOHs with ethylene signaling. Recently, Huang et al. (2019) reported the importance of ethylene signaling in survival of rice seedling under submergence. They suggested that pretreatment with the ethylene precursor, ACC under submergence stress affects intracellular redox homeostasis and antioxidant systems and improves the tolerance of rice seedlings to complete submergence.

In rice, ROS mediates ethylene-induced adventitious root growth and parenchyma cell death, resulting in aerenchyma formation (Bailey-Serres and Voesenek, 2008; Steffens and Sauter, 2009; Steffens et al., 2006, 2013). Ethylene-induced adventitious root growth in response to submergence is controlled by ROS generated at the plasma membrane during stress condition in deepwater rice (Steffens et al., 2012). It is interesting to note that ethylene-treated (150 μM ethephon) adventitious root primordia were enhanced by ROS (H_2O_2) production in comparison with non-treated plants, suggesting that ethylene-induced growth of root primordia is dependent on ROS homeostasis and/or production. Application of ACC, an ethylene precursor (1, 10, and 100 μM) also confirmed that ethylene regulates growth of isolated root primordia. Interestingly, studies using inhibitors (potassium iodide and 3-amino-1,2,4-triazole, an H_2O_2 scavenger and catalase inhibitor, respectively) indicated that ethylene-induced adventitious root growth is mediated by ROS activity of antioxidant enzymes. Ella et al. (2003a) studied the importance of ROS in the recovery after complete submergence in rice. They found that recovery is based on higher level of ascorbate-glutathione antioxidant enzymes activity during recovery. The tolerant genotype (FR13A) had higher activity of GR and ascorbate content, which more efficiently helped in detoxification of ROS in tolerant genotype compared to the sensitive genotype (IR42). Interestingly, an ERF (*BnERF2*.4) from *Brassica napus* (Rapeseed) played a central role in the regulation of submergence stress responses in Arabidopsis. Over-expression of the antioxidant genes (*Fe-SOD*, *Cu/Zn-SOD*, and *POD*) in transgenic Arabidopsis showed that ERF *BnERF2.4* potentiates the antioxidant enzymes, scavenges ROS accumulation, and protects plants from submergence-induced oxidative damages (Lv et al., 2016). In Arabidopsis plants recovering from prolonged submergence, the reoxygenation was linked with increased ethylene production and excessive ROS formation, since the plants are rapidly exposed to light and high O_2 (Yeung et al., 2018). The authors proposed that ethylene plays an important role in ROS amelioration that occurs during subsequent reoxygenation (Yeung et al., 2019). From these studies it can be concluded that ethylene effects ROS metabolism and the antioxidant system to prevent cell injury caused by submergence induced oxidative stress (Fig. 3; 4). However, the current knowledge on how plants cope with cellular imbalances induced by flooding stress and ethylene-ROS-defense systems interaction needs more investigations to use this knowledge for improving flooding tolerance.

4. Involvement of ethylene in aerenchyma formation and cell wall degradation under flooding stress

Aerenchyma is an internal gas transport system that delivers gases to lower stem and roots, including O_2. This is accomplished via convection and diffusion through the lacunae of the aerenchyma. Under flooding, plants survival is dependent on the formation of aerenchyma to supply $O_2$to roots (Evans, 2003; Jackson, 2008; Yamauchi et al., 2016). Aerenchyma formation is constitutively induced during root

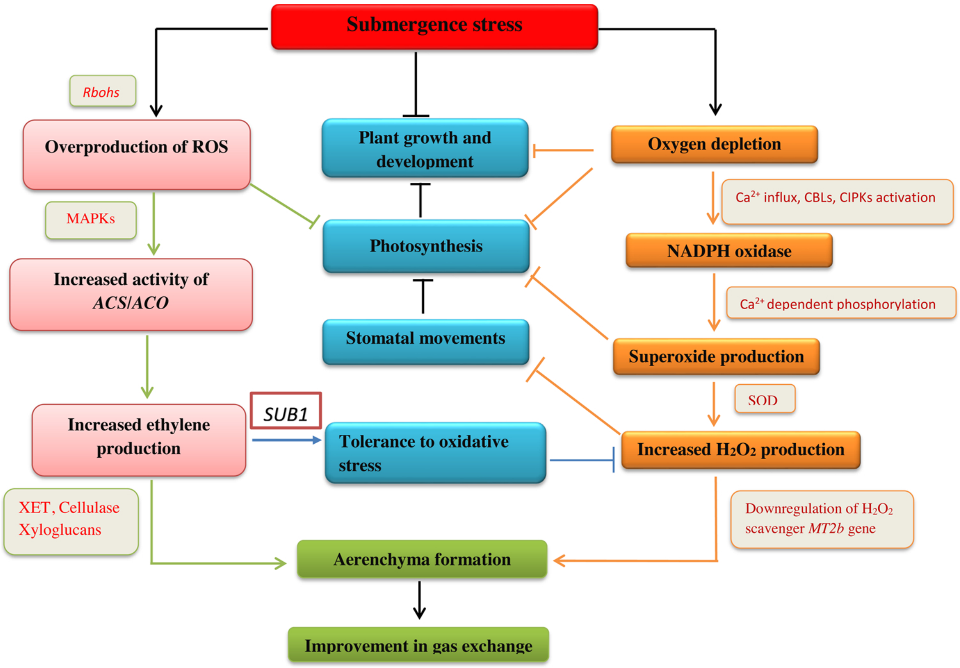

Fig. 3. An overview of submergence stress that induces overproduction of ROS or limited oxygen availability. These conditions inhibit photosynthesis, plant growth and development at different scales. Low oxygen stress generates more peroxides, which in turn effects plants growth and development by damaging cell membranes and inhibiting various critical physiological processes necessary for survival. Overproduction of ROS, stimulates the activity of genes associated with ethylene production by activating MAPKs. The arrows indicate positive regulation whereas the T-bars represent inhibitory effects. ACS/ACO; 1-aminocyclopropane-1-carboxylate synthase/oxidase, MAPK; mitogen activated protein kinase, NADPH; nicotinamide adenine dinucleotide phosphate, ROS; reactive oxygen species, H_2O_2; hydrogen peroxide, Rbohs; respiratory burst oxidase homologs; *SUB1*; Submergence 1, XET; xyloglucan endo-transglycosylase, SOD; superoxide dismutase, CBLs; Calcineurin-B-like proteins, CIPKs ; CBL-interacting protein kinases, MT2B; Metallothionein-like protein 2B.

development in rice, but under limited O_2availability caused by flooding, formation of aerenchyma is enhanced in several plant species. This adaptation strategy is regulated by ethylene, which induces several changes in plant morphology and physiology (Yu et al., 2009; Yin et al., 2013). Ethylene has been considered the key regulator of the formation of aerenchyma in *Zea mays* (maize) (Drew et al., 2000) and rice (Fukao and Bailey-Serres, 2008a, b), induced through programmed cell death (PCD) of specific root cortical cells. In rice, ethylene biosynthesis increases soon after submergence, with limited effect of reoxygenation (Raskin and Kende, 1984; Fukao and Bailey-Serres, 2008a), and the internodes produce four times more ethylene under submergence than in air (Raskin and Kende, 1984; Fukao and Bailey-Serres, 2008a).

Not all plants are capable of developing aerenchyma tissue; only few species like semi-aquatic plants like rice and to lesser extent, some crops like maize retain the capacity. Yu et al. (2009) reported that application of different concentrations of ethephon (0, 0.4, 4, 40, 400 mg L^{-1}) to rice plants alters aerenchyma formation by disintegrating cells in mediopellis. With the increasing ethephon concentrations from 0 to 400 mg L^{-1}, there was a significant increase in the number of deformed cells in the middle cortex. Ethephon concentration at 400 mg L^{-1} appeared to distort and collapse the cortex without disintegration of cell walls and aerenchyma formation. Whereas, concentration of 0.4 mg L^{-1} ethephon induced the development of rice lateral root primordia. Yukiyoshi and Karahara (2014) showed the involvement of ethylene signaling in aerenchyma formation in submerged rice roots and noted that total aerenchyma area was increased after treatment with 1 μM ACC, whereas treatment with 1-MCP (the ethylene action inhibitor, 0.1 or 1 ppm) blocked ethylene-induced aerenchyma formation. Parlanti et al. (2011) analyzed ethylene-mediated formation of aerenchyma in two rice varieties, FR13A (having *SUB1A* gene and limited growth under submergence) and Arborio Precoce (a fast elongation rice variety under submergence) to show contrast in flooding response in terms of internode elongation and survival. Arborio Precoce, exhibited active ethylene biosynthetic machinery associated with increased aerenchyma formation, whereas, FR13A displayed increased aerenchyma formation without increase in ethylene production. In a study focusing on maize root cortical cells during lysigenous aerenchyma formation, the main cell wall modification enzymes identified were xyloglucan endo-transglycosylase (XET), polygalacturonase, expansins, and cellulase. These enzymes were upregulated under waterlogging and repressed in maize plants treated with 1-MCP (Rajhi et al., 2011). Taken together, we could conclude that ethylene modulates aerenchyma formation under flooding conditions, but more studies are needed to understand the mechanism by which this effect is mediated.

Ethylene was also known to trigger cell wall degrading enzymes, particularly cellulase (He et al., 1996). The activity of this enzyme is required for cell wall degradation and dissolution essential for aerenchyma formation (Gunawardena et al., 2001). In earlier studies on *Helianthus annuus* (sunflower), cellulase activity was reported to be associated with aerenchyma formation (Kawase, 1979). The activity of this enzyme increases several hours after ethylene induction and is regulated by ethylene. The highest cellulase activity was observed after 8 days in maize plants exposed to hypoxia (4% O_2) or 1 μL L^{-1} of ethylene. The role of ethylene was demonstrated by treating the plants with ethylene biosynthesis inhibitors such as AVG, which also inhibits cellulase activity under hypoxia (He et al., 1994). Cell wall breakdown usually occurs 12 h after loss of cell turgor and disappearance of vacuoles. The aerenchyma formation is completed when the lacunae is formed and filled with gases. Hydrophobic compounds are also produced around the cavities to avoid water filling. Besides cellulase, other cell wall degrading enzymes are also involved during the last stage of aerenchyma formation. Indeed, cell wall degradation is a combined action of pectolytic, xylanolytic, and cellulosolytic enzymes, in particular xyloglucan, XET, pectinases, and expansins (Evans, 2003). Ethylene is an inducer of these enzymes and it has been widely demonstrated in senescence studies of fruits and leaves. Ethylene-induced upregulation of expansins has been shown before (Rose et al., 2000) and in maize roots, XET expression increased after exposure to hypoxia for 12 h under flooded conditions (Saab and Sachs, 1996). In maize, the pectinase and xylanase enzymes were induced after three days of partial flooding, especially in adventitious roots, while cellulase enzyme activity was detected after seven days (Bragina et al., 2003).

5. Involvement of ethylene in regulation of underwater photosynthesis and related leaf traits

Studies have revealed that ethylene has a strong impact on photosynthesis under different abiotic stresses (Khan et al., 2015; Thao et al., 2015; Khan et al., 2017). During submergence, the rate of diffusion of O_2 and CO_2 between the plant and its environment is significantly

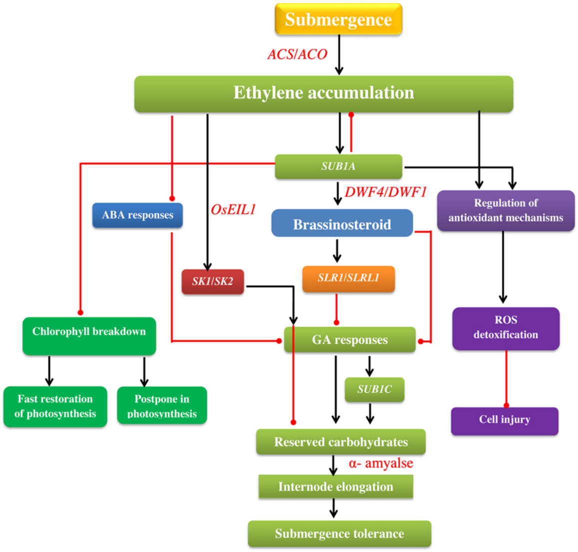

Fig. 4. Submergence induces enhanced transcript levels of ethylene biosynthetic genes (*ACS* and *ACO*) leading to ethylene accumulation, here we take rice as an example. Accumulation of ethylene mediates tolerance through the *SUB1A* gene. Ethylene initiates accumulation of SKs, *SLRI*, *SLRL1* and *SUB1A*. *SK1* and *SK2* are induced by enhanced expression of *OsEIL1a* during ethylene accumulation, which binds to the promoter of *SK1* and *SK2* thereby increasing their transcript levels, which in turn increase accumulation of bioactive GA in submerged internodes, causing plant shoots to elongate fast and escape submergence. *SLRI* and *SLRL1* are negative regulators of GA responses and are regulated by *SUB1*A through brassenosteriods (BR) to suppress growth and conserve carbohydrates. Ethylene also negatively regulates ABA responses leading to inhibition of GA and conservation of carbohydrates. In addition, ethylene also takes part in regulation of antioxidant machinery and ROS detoxification by inducing enzymes like SOD and CAT, either through *SUB1A* or by direct action. *SUB1A* controls the breakdown of photosynthetic pigments through suppression of ethylene, improving underwater photosynthesis and accelerating the recovery process upon desubmergence. The black arrow lines indicate positive regulation whereas red lines represent inhibitory effects. ACS/ACO; 1-aminocyclopropane-1-carboxylate synthase/oxidase, OsEIL1; *O. sativa* ethylene insensitive 3-like, SOD; superoxide dismutase, CAT; catalase, SK1/SK2; Snorkel 1/2, SLR1; Slender Rice-1, SLRL1; Slender Rice- Like 1 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

reduced, which causes hypoxic and sometimes anoxic condition, resulting in inhibition of photosynthesis and growth (Setter et al., 1989; Pellegrini et al., 2017; Winkel et al., 2014, 2016). Li et al. (2010) reported that submergence significantly reduced net photosynthetic rate, intrinsic water use efficiency, and stomatal conductance in *Pterocarya stenoptera* (Chinese wingnut) seedlings. When completely submerged, plants undergo the formation of gas films on hydrophobic leaves to enhance gas exchange between leaves and floodwater. This, will subsequently increase internal aeration by facilitating the entry of O_2 from floodwater when in the dark, and CO_2 entry for photosynthesis when in light (Pedersen et al., 2009; Ismail, 2018). Several studies established the role of gas films in rice submergence tolerance using artificially induced variation or loss-of-function mutants (Pedersen et al., 2009; Winkel et al., 2013; Kurokawa et al., 2018). Winkel et al. (2014) investigated underwater photosynthesis in relation to the *SUB1* gene. They found that under complete submergence, gas film retention is important for underwater photosynthesis in several rice cultivars (FR13A, Swarna, IR42 and Swarna-Sub1). Underwater photosynthesis markedly decreased when gas films are removed, suggesting their significant role in gas exchange during submergence. FR1A, the submergence tolerant landrace, retained underwater photosynthesis for longer duration and marked decline in this ability was observed in the sensitive genotypes.

Submergence tolerance was also reported to be associated with duration of retention and volume of gas films during submergence in some plant species, and recently Leaf Gas Film 1*(LGF1*) associated with formation and retention of gas films underwater was cloned and characterized (Kurokawa et al., 2018). A complementation test of *LGF1* expressed in the *drp7* mutant background, verified the gene function in regulating underwater photosynthesis, leaf hydrophobicity and abundance of wax platelets. Understanding the role of ethylene during flooding and its potential involvement in retention and persistence of leaf gas films could be beneficial during prolonged submergence.

Recently, Alpuerto et al. (2016) evaluated the role of *SUB1* during de-submergence through modulation of ROS metabolism and dehydration. They noted that submergence significantly inhibit photosystem II activity and causes breakdown of proteins and accumulation of amino acids to similar extent in the two near isogenic lines, submergence-sensitive M202 and tolerant M202-*Sub1*. But, upon de-submergence, M202-*Sub1* recovers faster. Several previous studies established the positive role of *SUB1A* during recovery of photosynthesis and regrowth after prolonged submergence using near-isogenic lines contrasting in *SUB1* gene (Singh et al., 2009, 2014; Ismail et al., 2013; Ismail and Atlin, 2019). Further studies are needed to establish the mechanisms by which *SUB1* enhances this recovery rate, and whether this response is influenced by other introgressions from the donor parent.

6. An ethylene-response factor like gene; *SUB1* imparts major role in complete submergence tolerance in rice

SUB1 controls many adaptive mechanisms in submergence stress by regulating internode elongation, carbohydrate consumption, maintenance of photosynthetic pigments, and ethanolic fermentation in rice (Fukao et al., 2006; Singh et al., 2014) and is likely involved in regrowth and recovery when water recedes (Fukao et al., 2006; Xu et al., 2006). Two alleles of *SUB1* are invariably present in the *SUB1* locus in all accessions of rice analyzed so far, *SUB1B* and *SUB1C,* while the presence of *SUB1A* is variable. For instance, *SUB1B* and *SUB1C* are present in both *indica* and *japonica* accessions, whereas *SUB1A* is limited to *indica* accessions (Xu and Mackill, 1996; Fukao et al., 2006, 2009; Xu et al., 2006). *SUB1A-1* is the functional allele that encodes an ERF transcription factor and consequently controls flooding tolerance in rice (Fukao et al., 2006, 2009; Xu et al., 2006). Several studies have shown that tolerance of complete submergence in rice is conferred by the *SUB1A-1* allele (Xu et al., 2006; Jung et al., 2010; Bailey-Serres et al., 2010). About 898 genes were identified that are dependent on *SUB1A*-mediated responses, including regulation of anaerobic respiration, hormonal responses, and ROS scavenging systems in the tolerant M202-*Sub1* (Jung et al., 2010). The authors focused on a set of transcriptional regulators belonging to the AP2/ERF family that shows association with the *SUB1A-1*-regulated responses, confirming the impact of *SUB1A-1* on various pathways involved in submergence tolerance. All released rice varieties cannot withstand submergence for over 5 days, with few landraces such as FR13A, FR13B, Thavalu, and Goda Heenati (Ismail and Mackill, 2013), can survive over 2 weeks of complete submergence by restricting shoot elongation underwater, and preserving carbohydrates for maintenance metabolism and recovery when de-submerged (Ella et al., 2003b; Xu et al., 2006; Fig. 4). Two alleles were discovered for *SUB1A* and only genotypes carrying the *SUB1A-1* allele are found to be submergence tolerant, whereas genotypes containing the *SUB1A-2* or lacking the *SUB1A* gene are intolerant (Septiningsih et al., 2009; Singh et al., 2010). Furthermore, Singh et al. (2010) showed that genotypes carrying the *SUB1A*-1 allele together with *SUB1C*-3 or *SUB1C*-1 were tolerant, whereas genotypes carrying *SUB1A-2* allele together with the *SUB1C*-1 or *SUB1C-3* allele are intolerant. Sarkar and Bhattacharjee (2011) reported that, both *SUB1A* and *SUB1C* are crucial for submergence tolerance in rice, which was not confirmed in subsequent studies. In recent studies, the dual role of *SUB1* has been demonstrated in regulating root and shoot growth, which in turn enhances plants survival rates under submergence. In this study, the rate of shoot elongation declined with simultaneous enhancement in root growth and activity within the tolerant genotypes Swarna-*Sub1* and FR13A during submergence. Also, after submergence, the root injury decreased, with low malondialdehyde production and reduction in electrolyte leakage, with higher concentrations of starch reported in roots and shoots of tolerant genotypes (Bui et al., 2019). Singh and Sinha (2016) reported enhanced activities of MITOGEN ACTIVATED PROTEIN KINASE 3 (MPK3) in a *SUB1A*-dependent manner and imparts in submergence tolerance in rice. They confirmed the physical interaction of MPK3 with *SUB1A* and phosphorylates specific to tolerant-allele and the expression of MPK3 is positively regulated by *SUB1A-1* during submergence. Using marker assisted backcrossing, the *SUB1* gene was introgressed in several rice mega varieties, conferring submergence tolerance, such as IR64-*Sub1* (Singh et al., 2009; Septiningsih et al., 2009), Samba Mahsuri-*Sub1* (Singh et al., 2009), Thadokkam1-*Sub1*, and BR11-*Sub1* (Iftekharuddaula et al., 2011), all of which has been released for commercial used by farmers in India, Nepal, Bangladesh, Indonesia and the Philippines, with considerable impacts on productivity in flood-prone areas (Mackill et al., 2012; Ismail et al., 2013; Ismail and Atlin, 2019). These studies clearly established that *SUB1*–as an ERF element, has significantly helped in enhancing stabilizing yields of rice in areas frequently affected by flash floods or submergence (Ismail and Atlin, 2019).

7. Ethylene and its crosstalk with phytohormones and other signaling molecules under flooding stress

During flooding stress, ethylene accumulation and its signaling pathways display a complex interplay with other important signaling molecules such as nitric oxide (NO), ROS, Ca^{2+}, and CO_2 for fine tuning plant adaptive responses (Sasidharan et al., 2018). The reduction in gas diffusion caused by floodwater leads to the accumulation of ethylene and NO but unlike ethylene, NO is short lived, highly reactive and show limited accumulation. Both ethylene and NO gases affect each other during the course of flooding (Magalhaes et al., 2000; Liu et al., 2017) and their crosstalk is facilitated by phytoglobins or ERF-VIIs (Mira et al., 2016; Sasidharan et al., 2018). ERF-VIIs have turned up as a critical mechanism for NO sensing during flooding highlighting their role and proteolytic control in gaseous signal transduction (Gibbs et al., 2014). Phytoglobins modulate NO and ethylene concentration during flooding; however both gaseous compounds in turn, influence phytoglobins abundance. Additionally, ethylene entrapment is a rapid signal detected by the plants upon submergence, allowing acclimation to forthcoming hypoxic conditions through the enhancement of phytoglobin1 (*PGB1*) expression and rapid NO depletion; which leads to ERF-VII accumulation (Hartman et al., 2019). Under hypoxic condition, transgenic maize roots overexpressing a NO-scavenging phytoglobin (*ZmPgbs*) showed the lowest level of ethylene as well as a reduction in ROS staining, while showing the highest growth (Mira et al., 2016). These results suggest that phytoglobins play important role in protecting root apical meristems from hypoxia-induced PCD caused by NO-mediated accumulation of ethylene and subsequent overproduction of ROS. The identification of this sensing mechanism that pre-adapts plants to survive subsequent hypoxia depends on ethylene signaling and its ability to increase the stability of ERF-VII proteins (Perata, 2019), paving the way for genetic manipulation of ethylene responsiveness of *PGB1* genes to enhance conditional flooding tolerance in crops.

Regulated ROS production is another important signal for triggering adaptive responses during flooding-induced hypoxia (Yamauchi et al., 2017). ROS production is tightly regulated by interactions of multiple proteins including HRU1, an ERF-VII target protein that coordinates O_2 sensing with ROS production via NADP oxidases (Gonzali et al., 2015; Sasidharan et al., 2018). Also, ROS and ethylene signaling functionally interact with plants adaptive responses to hypoxic conditions, such as lysigenous aerenchyma formation (Yamauchi et al., 2017), adventitious root growth (Steffens et al., 2012), and gas filled void formation. Calcium dependent signaling pathways are also involved in ethylene responsive formation of lysigenous aerenchyma (He at al., 1996; Rajhi et al., 2011). The expression of genes associated with Ca^{2+} signaling such as CBL, Ca/CaM dependent protein kinases are also modulated during flooding (Rajhi et al., 2011).

Phytohormones play a major role in overall signaling mechanisms during flooding stress conditions in plants predominated by the crosstalk between ethylene with other phytohormones such as auxin (Lorbiecke and Sauter, 1999), gibberellic acid (GA; Voesenek et al., 2003), abscisic acid (ABA; Benschop et al., 2005), jasmonic acid (JA; Lorenzo et al., 2003), and BR (Van de Poel et al., 2015; Jiroutova et al., 2018). There is an intricate network of hormonal dependent survival mechanisms that is important for physiological processes during submergence stress. For instance, AUX/IAA mediated auxin signaling is possibly involved in ethylene dependent aerenchyma formation in rice roots under O_2 deficient conditions during waterlogging (Yamauchi et al., 2020). The *iaa13* rice mutant with suppressed auxin signaling exhibits lower aerenchyma formation under O_2 deprived conditions along with the reduced expression of genes associated with ethylene biosynthesis. Also, an auxin transport inhibitor N-1-naphthylphthalamic acid (NPA) inhibits root elongation under O_2 deprived conditions, reduces transcript levels of *ACS1* and *ACO5* and with absolute inhibition of aerenchyma formation in rice further supporting the role of auxin in ethylene dependent aerenchyma formation (Yamauchi et al., 2020). In deepwater rice the rapid increase in ethylene biosynthesis under submerged conditions, stimulates mRNA accumulation of two group VII ERF genes: *SNORKEL1* (SK1) and *SNORKEL2* (SK2) (Hattori et al., 2009; Fukao and Bailey-Serres, 2008a) which in turn triggers internode elongation by enhancing endogenous levels of bioactive GA (Ayano et al., 2014). Similarly, ethylene accumulation upon submergence in *R. palustris* initiates elongation through the down regulation of ABA and the stimulated action of GA (Benschop et al., 2005; 2006).

Plant species and genotypes that adopt a quiescence strategy to survive transient completed submergence enter into a state of inactivity, which minimizes O_2 consumption and preserves stored carbohydrates until floodwater drawdown (Voesenek and Bailey-Serres, 2015; Akman et al., 2012). In submergence tolerant lowland rice cultivars like FR13A, ethylene accumulation co-regulates anaerobic metabolism through induction of *SUB1A* (Fukao et al., 2006; Xu et al., 2006). *SUB1A* suppresses GA biosynthesis and responsiveness by regulating two GA signaling suppressors, *SLENDER RICE-1* (*SLR1*) and *SLR1 like 1* (*SLRL1*), to restrict shoot elongation under submergence (Fukao and Bailey-Serres, 2008b). Overexpression of *SUB1A* limits starch breakdown and carbohydrate metabolism (Fukao et al., 2006) while enhancing fermentation to improve acclimation of plants to flood conditions (Fukao et al., 2006).

In support of the mechanistic regulations of ERF family, Gao et al. (2011) reported that, the mechanisms affected by *SUB1A* and *SK*-mediated tolerance is dependent upon ethylene and GA interaction and critical for plant growth, development, and adaptation to stress. In deepwater rice high concentrations of GA promotes rapid internode and leaf elongation; and the alteration in GA-signaling mechanism is the result of increased protein concentrations of the GA signal repressing GRAS family of TFs, including SLR1 and SLRL1 during submergence. The authors demonstrated that transgenic lines response ectopically expressing *SUB1A* to significantly limit underwater elongation and suppress GA content in *SUB1A*-expressing plants (Fukao and Bailey-Serres, 2008a, b).

Numerous studies have shown that in submerged plants, ethylene, GA and ABA are involved in regulation of processes such as shoot elongation and carbon mobilization (Kende et al., 1998; Sauter, 2000; Voesenek et al., 2003). Wu et al. (2019) showed crosstalk between phytohormones (ABA, IAA, GAs, and ZR; trans-zeatin-riboside) that regulates physiological responses to submergence stress using IR64 and

IR64-Sub1 rice genotypes. Genotype IR64 showed more sensitivity towards submergence stress with increase of leaf GAs, ABA, IAA contents and the expression of *OsCPS1*, *OsGA20ox1* and *OsIAA11*, in contrast IR64-*Sub1* had significantly decreased hormones content with prolonged stress. Treatment of these two rice varieties with ACC under submergence caused leaf yellowing, shoot elongation, and leaf senescence, with increased GAs and IAA concentrations and enhanced expression of *OsCPS1*, *OsGA20ox1* and *OsIAA11*. Paclobutrazol (PB; an antagonist of GA) treatment resulted in contrast effects with reduction in GA concentration and inhibition of underwater shoot elongation and leaf senescence, with concurrent increase in ZR. As a quiescent strategy in rice genotypes, *SUB1* gene expression is enhanced by ethylene, causing over accumulation of repressors of GA signaling, *SLR1* and *SLRL1* (Bashar et al., 2019). The indirect involvement of ethylene in GA signaling mediated via *SUB1*- dependent pathway is clearly demonstrated by these studies.Kuroha et al. (2018) furthermore, confirmed the interaction of ethylene signaling and gibberellin biosynthesis in deepwater rice. OsEIL1a, an ethylene-responsive transcription factor activates *SD1* gene that regulates internode elongation in rice to scape submergence stress. During submergence, GA_3 treatment of FR13A induced elongation growth under water and compromised survival, indicating that GA-regulated processes exhibit adverse impact on tolerance to prolonged submergence (Ella et al., 2003b; Das et al., 2005). Ethylene regulates GA and ABA, which are involved in shoot elongation as positive and negative regulators, respectively. ABA concentration decreased (Benschop et al., 2005; Fukao and Bailey-Serres, 2008b), while endogenous GA increased (van der Straeten et al., 2001; Fukao and Bailey-Serres, 2008b) following increase in ethylene concentration under submergence. Decrease in ABA is considered imperative for submergence-induced GA responsiveness and promotes internode or petiole elongation (Kende et al., 1998; Benschop et al., 2006). In *Rumex palustris* (marsh dock), reduced ABA and enhanced GA biosynthesis were seen in response to submergence and was associated with shoot elongation and leaf growth to emergence from floodwater (Benschop et al., 2006).

Ethylene stimulates shoot elongation as a strategy to escape low O_2 conditions (Voesenek and Blom, 1999). It acts as a signal in several parallel pathways required for rapid underwater shoot elongation. Accumulated ethylene inhibits 9-cis-epoxycarotenoid dioxygenase (*NCED*) expression, an enzyme involved in ABA biosynthesis and also results in breakdown of ABA into phaseic acid, thereby decreasing ABA (Benschop et al., 2005; Saika et al., 2007). This reduction in ABA concentration interferes with GA pathway leading to rapid shoot elongation under submergence, as seen in marsh dock (Benschop et al., 2006) and rice (Kende et al., 1998). In marsh dock, reduction in ABA triggers the expression of GA 3-oxidase required for formation of bioactive GA, thereby stimulating shoot elongation (Benschop et al., 2006). In rice, during low ABA, internodes become sensitive to GA, thereby stimulating shoot elongation (Kende et al., 1998). Ethylene also induces the expression of genes such as *EXPA* and *EXPB*, which encodes expansin proteins controlling cell wall extensibility and aiding in rapid cell division during shoot elongation under submergence (Kim et al., 2000; Vriezen et al., 2000; Vreeburg et al., 2005). *SUB1A* genotypes also respond to jasmonate and salicylic acid (SA) mediated leaf senescence. Moreover, ethylene biosynthesis accelerated senescence stimulated by darkness and jasmonate, while *SUB1A* controls dark-induced ethylene accumulation, thereby inhibiting the breakdown of carbohydrates and chlorophyll, both of which are important for tolerance of submergence, drought, and oxidative stress (Fig. 4). Studies including quantitative trait loci (QTL) mapping are being conducted to identify new submergence tolerant QTLs that could act additively to *SUB1* in to further enhance submergence tolerance in rice. Amin et al. (2018) identified three accessions (Lakhi, Atshotti and Damsi) with tolerance similar to that FR13A. Few other accessions like Putidepa, DSL-78 − 8, and Sadadanga boro also showed tolerance of submergence but are lacking the indel markers, GnS2 and Sub1C173 specific for the *SUB1*locus, suggesting that these accessions are potential sources of new genes for tolerance.

Jung et al. (2010) identified four genes associated with cell growth and five genes associated with GA biosynthesis and predicted the activation of GA2ox1 and four genes encoding repressors of cell growth and restriction of underwater shoot elongation, all of which belongs to AP2/ERF TFs (*Os04g48350, Os02g45450, Os09g35010, Os09g35020*) in the tolerant lines. Another interesting crosstalk under submergence was the role played by cytokinins in delaying ethylene-induced senescence during submergence (Balibrea Lara et al., 2004). The role of cytokinin in regulating the action of *SUB1A*-1 was speculatively interpreted as cytokinin mediated delayed senescence via accumulation of ethylene during submergence (Jung et al., 2010). Schmitz et al. (2013) reported that *SUB1A* enhances the degradation of GA, mediated through induction of BR in rice under submergence. The increase in BR contributes to the accumulation of DELLA protein SLR1 and acts negatively on GA signaling, reducing shoot elongation. Processes such as hyponastic curvatures and elongation of petioles are necessary for submergence tolerance (Cox et al., 2006). Molecular mechanisms associated with these hormonal cross talks are poorly understood, and more research is required to decipher the genetic bases of these interactions to clearly unravel the mechanisms underlying flooding response, and to facilitate breeding more resilient crops, especially with the recent increase in intensity and frequency of floods associated with climate change.

8. Conclusion and future perspectives

The frequency and intensity of floods are increasing steadily worldwide as one of the serious climate change adversities. Understanding the processes involved in plant responses and adaptation to flooding is becoming progressively more important to enhance resilience of crop plants under these new weather conditions and to sustain food production. The gaseous phytohormone ethylene plays notable roles in plant adaptation to excess water condition by regulating several processes that influence plant growth and survival, including signaling pathways and metabolic adjustments. Significant progress was made in understanding the basic physiological and molecular mechanisms associated with ethylene-mediated plant responses to flooding, though this knowledge is still incomplete. Here we provided examples from rice as the model crop and few other plant species. Rice is adapted for growth under flooded soil conditions, but less so under deeper water that leads to partial or complete submergence of the shoot. Ethylene modulates rice adaptation to transient flash floods through ethylene responsive factor elements underlying *SUB1A* gene that confer tolerance of complete submergence through suppression of shoot growth. The snorkel genes (*SK1* and *SK2*) exert juxtaposing effect by triggering internode elongation under prolonged deepwater conditions to bring the shoot in contact with air and facilitate gas exchange. Ethylene also influence other processes essential for plant survival of flooded conditions such as retention of chlorophyll, dampening the effects ROS and enhancing underwater photosynthesis. This cascade of processes is mediated through interaction and crosstalk with several other plant hormones, including gibberellins, ABA, cytokines, and BR, and with signaling molecules. Advancing the knowledge of ethylene perception and signaling during flooding could lead to further dissection of metabolic and genetic pathways for adaptation to flooding stress, and will ultimately help in breeding resilient crop species and varieties that are more resilient and adapted to the increasing flooding caused by changes in rainfall patterns and sea level rise associated with climate change.

Authors statement

All authors contributed significantly, read and approved the article

Declaration of Competing Interest

Authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.envexpbot.2020.104188.

References

Akman, M., Bhikharie, A.V., McLean, E.H., Boonman, A., Visser, E.J.W., Schranz, M.E., van Tienderen, P.H., 2012. Wait or escape? Contrasting submergence tolerance strategies of *Rorippa amphibia*, *Rorippa sylvestris* and their hybrid. Ann. Bot. 109, 1263–1276.

Alpuerto, J.B., Hussain, R.M.F., Fukao, T., 2016. The key regulator of submergence tolerance, SUB1A, promotes photosynthetic and metabolic recovery from submergence damage in rice leaves. Plant Cell Env 39, 672–684.

Amin, A., Iftekharuddaula, K.M., Sarker, A., Talukder, A.H., Ghoshal, S., Shalahuddin, A.K.M., Aditya, T.L., Ali, M.A., Collard, B., 2018. Identification of novel submergence tolerant local rice cultivars of Bangladesh. Int. Jour. Gen. Geno 6, 44–51.

Armstrong, W., 1979. Aeration in higher plants. In: Woolhouse, H.W. (Ed.), Advances in Botanical Research. Academic Press, London, pp. 225–332.

Ayano, M., Kani, T., Kojima, M., Sakakibara, H., Kitaoka, T., Kuroha, T., Angeles-Shim, R.B., Kitano, H., Nagai, K., Ashikari, M., 2014. Gibberellin biosynthesis and signal transduction is essential for internode elongation in deepwater rice. Plant Cell Environ. 37, 2313–2324.

Bailey-Serres, J., Voesenek, L.A.C.J., 2008. Flooding stress: acclimations and genetic diversity. Annu. Rev. Plant Biol. 59, 313–339.

Bailey-Serres, J., Fukao, T., Ronald, P., Ismail, A., Heuer, S., Mackill, D., 2010. Submergence tolerant rice: *SUB1*'s journey from landrace to modern cultivar. Rice 3, 138–147.

Bailey-Serres, J., Fukao, T., Gibbs, D.J., Holdsworth, M.J., Lee, S.C., Licausi, F., Perata, P., Voesenek, L.A.C.J., van Dongen, J.T., 2012. Making sense of low oxygen sensing. Trends Plant Sci. 17, 129–138.

Balibrea Lara, M.E., Gonzalez-Garcia, M.-C., Fatima, T., Ehneß, R., Lee, T.K., Proels, R., Tanner, W., Roitsch, T., 2004. Extracellular invertase is an essential component of cytokinin mediated delay of senescence. Plant Cell 16, 1276–1287.

Banga, M., Slaa, E.J., Blom, C.W.P.M., Voesenek, L.A.C.J., 1996. Ethylene biosynthesis and accumulation under drained and submerged conditions (a comparative study of two *Rumex* species). Plant Physiol. 112, 229–237.

Bashar, K.K., Tareq, M.Z., Amin, M.R., Honi, U., Tahjib-Ul-Arif, M., Sadat, M.A., Hossen, Q.M.M., 2019. Phytohormone-mediated stomatal response, escape and quiescence strategies in plants under flooding stress. Agronomy 9, 43.

Baxter, A., Mittler, R., Suzuki, N., 2014. ROS as key players in plant stress signalling. J. Exp. Bot. 65, 1229–1240.

Benschop, J.J., Jackson, M.B., Guhl, K., Vreeburg, R.A.M., Croker, S.J., 2005. Contrasting ¨ interactions between ethylene and abscisic acid in *Rumex* species differing in submergence tolerance. Plant J. 44, 756–768.

Benschop, J.J., Bou, J., Peeters, A.J.M., Wagemaker, N., Guhl, K., Ward, D., 2006. Long-term submergence-induced elongation in *Rumex palustris* requires abscisic acid-dependent biosynthesis of gibberellin. Plant Physiol. 141, 1644–1652.

Bragina, T.V., Rodionova, N.A., Grinieva, G.M., 2003. Ethylene production and activation of hydrolytic enzymes during acclimation of maize seedlings to partial flooding. Russ. J. Plant Physiol. 50, 794–798.

Bui, L.T., Ella, E.S., Dionisio-Sese, M.L., Ismail, A.M., 2019. Morpho-physiological changes in roots of rice seedling upon submergence. Rice Sci 26, 167–177.

Cao, P., Jung, K.H., Choi, D., Hwang, D., Zhu, J., Ronald, P.C., 2012. The rice oligonucleotide array database: an atlas of rice gene expression. Rice 5, 17.

Catala, R., López-Cobollo, R., Mar Castellano, M., Angosto, T., Alonso, J.M., Ecker, J.R., Salinas, J., 2014. The Arabidopsis 14-3-3 protein RARE COLD INDUCIBLE 1A links low-temperature response and ethylene biosynthesis to regulate freezing tolerance and cold acclimation. Plant Cell 26, 3326–3342.

Clarke, S.M., Cristescu, S.M., Miersch, O., Harren, F.J.M., Wasternack, C., Mur, L.A.J., 2009. Jasmonates act with salicylic acid to confer basal thermotolerance in *Arabidopsis thaliana*. New Phytol. 182, 175–187.

Cox, M.C.H., Millenaar, F.F., Van Berkel, Y.E.M., Peeters, A.J.M., Voesenek, L.A.C.J., 2003. Plant movement. Submergence-induced petiole elongation in *Rumex palustris* depends on hyponastic growth. Plant Physiol. 132, 282–291.

Cox, M.C., Benschop, J.J., Vreeburg, R.A., Wagemaker, C.A., Moritz, T., Peeters, A.J., Voesenek, L.A., 2004. The roles of ethylene, auxin, abscisic acid, and gibberellin in the hyponastic growth of submerged *Rumex palustris* petioles. Plant Physiol. 136, 2948–2960.

Cox, M.C.H., Peeters, A.J.M., Voesenek, L.A.C.J., 2006. The stimulating effects of ethylene and auxin on petiole elongation and on hyponastic curvature are independent processes in submerged *Rumex palustris*. Plant Cell Environ. 29, 282–290.

Das, K.K., Sarkar, R.K., Ismail, A.M., 2005. Elongation ability and non-structural carbohydrate levels in relation to submergence tolerance in rice. Plant Sci. 168, 131–136.

Daszkowska-Golec, A., Szarejko, I., 2013. Open or close the gate – stomata action under the control of phytohormones in drought stress conditions. Front. Plant Sci. 4, 138.

Drew, M.C., 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Ann. Rev. Plant Physiol. Plant Mol. Biol 48, 223–250.

Drew, M.C., Jackson, M.B., Giffard, S., 1979. Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta 147, 83–88.

Drew, M.C., He, C.J., Morgan, P.W., 2000. Programmed cell death and aerenchyma formation in roots. Trends Plant Sci. 5, 123–127.

Ella, E.S., Kawano, N., Ito, O., 2003a. Importance of active oxygen-scavenging system in the recovery of rice seedlings after submergence. Plant Sci. 165, 85–93.

Ella, E.S., Kawano, N., Yamauchi, Y., Tanaka, K., Ismail, A.M., 2003b. Blocking ethylene perception enhances flooding tolerance in rice seedlings. Funct. Plant Biol. 30, 813–819.

Evans, D.E., 2003. Aerenchyma formation. New Phytol. 161, 35–49.

Fukao, T., Bailey-Serres, J., 2008a. Ethylene-a key regulator of submergence responses in rice. Plant Sci. 175, 43–51.

Fukao, T., Bailey-Serres, J., 2008b. Submergence tolerance conferred by Sub1A is mediated by SLR1 and SLRL1 restriction of gibberellin responses in rice. Pro. Nat. Acad. Sci. 105, 16814–16819.

Fukao, T., Xu, K., Ronald, P.C., Bailey-Serres, J., 2006. A variable cluster of ethylene response factor-like genes regulates metabolic and developmental acclimation responses to submergence in rice. Plant Cell 18, 2021–2034.

Fukao, T., Harris, T., Bailey-Serres, J., 2009. Evolutionary analysis of the Sub1 gene cluster that confers submergence tolerance to domesticated rice. Ann. Bot. 103, 143–150.

Fukao, T., Yeung, E., Bailey-Serres, J., 2011. The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. Plant Cell 23, 412–427.

Gao, W.J., Leung, K.T., Qin, W.S., Liao, B.Q., 2011. Effects of temperature and temperature shock on the performance and microbial community structure of a submerged anaerobic membrane bioreactor. Bioresour. Technol. Rep. 102, 8733–8740.

Gibbs, D.J., Lee, S.C., Isa, N.M., Gramuglia, S., Fukao, T., Bassel, G.W., Correia, C.S., Corbineau, F., Theodoulou, F.L., Bailey-Serres, J., et al., 2011. Homeostatic response to hypoxia is regulated by the N-end rule pathway in plants. Nature. 479, 415–418.

Gibbs, D.J., Isa, N.M., Movahedi, M., Lozano-Juste, J., Mendiondo, G.M., Berckhan, S., Marín-de la Rosa, N., Vicente Conde, J., Sousa Correia, C., Pearce, S.P., et al., 2014.). Nitric oxide sensing in plants is mediated by proteolytic control of group VII ERF transcription factors. Mol. Cell 53, 369–379.

Giuntoli, B., Perata, P., 2017. Group VII ethylene response factors in Arabidopsis: regulation and physiological roles. Plant Physiol. 176, 1143–1155.

Golicz, A.A., Schliep, M., Lee, H.T., Larkum, A.W.D., Dolferus, R., Batley, J., Chan, C.-K.K., Sablok, G., Ralph, P.J., Edwards, D., 2015. Genome-wide survey of the seagrass *Zostera muelleri* suggests modification of the ethylene signalling network. J. Exp. Bot. 66, 1489–1498.

Gonzali, S., Loreti, E., Cardarelli, F., Novi, G., Parlanti, S., Pucciariello, C., Bassolino, L., Banti, V., Licausi, F., Perata, P., 2015. Universal stress protein HRU1 mediates ROS homeostasis under anoxia. Nat. Plants 1, 15151.

Gunawardena, A.H.L.A.N., Pearce, D.M.E., Jackson, M.B., Hawes, C.R., Evans, D.E., 2001. Rapid changes in cell wall pectic polysaccharides are closely associated with early stages of aerenchyma formation, a spatially localized form of programmed cell death in roots of maize (*Zea mays* L.) promoted by ethylene. Plant Cell Environ. 24, 1369–1375.

Hartman, S., Liu, Z., van Veen, H., Vicente, J., Reinen, E., Martopawiro, S., Zhang, H., van Dongen, N., Bosman, F., Bassel, G.W., et al., 2019. Ethylene mediated nitric oxide depletion pre-adapts plants to hypoxia stress. Nat. Commun. 10, 4020.

Hartman, S., Sasidharan, R., Voesenek, L.A.C.J., 2020. The role of ethylene in metabolic acclimations to low oxygen. New Phytol. https://doi.org/10.1111/nph.16378.

Hattori, Y., Nagai, K., Furukawa, S., Song, X.J., Kawano, R., Sakakibara, H., Wu, J., Matsumoto, T., Yoshimura, A., Kitano, H., Matsuoka, M., Mori, H., Ashikar, M., 2009. The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 460, 1026–1030.

He, C.J., Drew, M.C., Morgan, P.W., 1994. Induction of enzymes associated with lysigenous aerenchyma formation in roots of *Zea mays* during hypoxia or nitrogen starvation. Plant Physiol. 105, 861–865.

He, C.J., Finlayson, S.A., Drew, M.C., Jordan, W.R., Morgan, P.W., 1996. Ethylene biosynthesis during aerenchyma formation in roots of maize subjected to mechanical impedance and hypoxia. Plant Physiol. 112, 1679–1685.

Hruz, T., Laule, O., Szabo, G., Wessendorp, F., Bleuler, S., Oertle, L., Widmayer, P., Gruissem, W., Zimmermann, P., 2008. Genevestigator v3: a reference expression database for the meta-analysis of transcriptomes. Adv. Bioinfo 2008, 420747.

Huang, Y., Yeh, T., Yang, C., 2019. Ethylene signaling involves in seeds germination upon submergence and antioxidant response elicited confers submergence tolerance to rice seedlings. Rice 12, 23.

Iftekharuddaula, K.M., Newaz, M.A., Salam, M.A., Ahmed, H.U., Mahbub, M.A.A., Septiningsih, E.M., Collard, B.C.Y., Sanchez, D.L., Pamplona, A.M., Mackill, D.J., 2011. Rapid and high-precision marker assisted backcrossing to introgress the sub1 QTL into BR11, the rainfed lowland rice mega variety of Bangladesh. Euphytica 178, 83–97.

Iqbal, N., Khan, N.A., Ferrante, A., Trivellini, A., Francini, A., Khan, M.I.R., 2017. Ethylene role in plant growth, development and senescence: interaction with other phytohormones. Front. Plant Sci. 8, 475.

Ismail, A.M., 2013. Flooding and submergence tolerance. In: In: Kole, C. (Ed.), Genomics and Breeding for Climate-Resilient Crops Vol 2. Springer-Verlag, Berlin Heidelberg, pp. 269–290. https://doi.org/10.1007/978-3-642-37048-9_7. Target Traits.

Ismail, A.M., 2018. Submergence tolerance in rice: resolving a pervasive quandary. New Phytol. 218, 1298–1300.

Ismail, A.M., Atlin, G., 2019. Incorporating stress tolerance in rice. In: Zeigler, R. (Ed.), Sustaining Global Food Security: The Nexus of Science and Policy. Part 3, Modern Plant Breeding; Chapter 13; Redesigning Crop Plants. CSIRO Publishing, Australia, pp. 224–246.

Ismail, A.M., Mackill, D.J., 2013. Response to flooding: submergence tolerance in rice. In: Jackson, M., Ford-Lloyed, B., Parry, M. (Eds.), Plant Genetic Resources and Climate Change - a 21st Century Perspective. CAB International, UK, pp. 251–269.

Ismail, A.M., Singh, U.S., Singh, S., Dar, M., Mackill, D.J., 2013. The contribution of submergence-tolerant (Sub1) rice varieties to food security in flood-prone areas. Field Crops Res. 152, 83–93.

Jackson, M.B., 2008. Ethylene-promoted elongation: an adaptation to submergence stress. Ann. Bot. 101, 229–248.

Jiroutova, P., Oklestkova, J., Strnad, M., 2018. Crosstalk between brassinosteroids and ethylene during plant growth and under abiotic stress conditions. Int. J. Mol. Sci. 19, 3283.

Jung, K.H., Seo, Y.S., Walia, H., Cao, P., Fukao, T., Canlas, P.E., Ronald, P.C., 2010. The submergence tolerance regulator Sub1A mediates stress-responsive expression of AP2/ERF transcription factors. Plant Physiol. 152, 1674–1692.

Juntawong, P., Sirikhachornkit, A., Pimjan, R., Sonthirod, C., Sangsrakru, D., Yoocha, T., Tangphatsornruang, S., Srinives, P., 2014. Elucidation of the molecular responses to waterlogging in Jatropha roots by transcriptome profiling. Front. Plant Sci. 5, 658.

Kawase, M., 1979. Role of cellulase in aerenchyma development in sunflower. Am. J. Bot. 66, 183–190.

Kazan, K., 2015. Diverse roles of jasmonates and ethylene in abiotic stress tolerance. Trends Plant Sci. 20, 219–229.

Kende, H., Van Der Knaap, E., Cho, H.T., 1998. Deepwater rice: a model plant to study stem elongation. Plant Physiol. 118, 1105–1110.

Khan, M.I.R., Iqbal, N., Masood, A., Khan, N.A., 2012. Variation in salt tolerance of wheat cultivars: role of glycinebetaine and ethylene. Pedosphere. 22, 746–754.

Khan, M.I.R., Nazir, F., Asgher, M., Per, T.S., Khan, N.A., 2015. Selenium and sulfur influence ethylene formation and alleviate cadmium-induced oxidative stress by improving proline and glutathione production in wheat. J. Plant Physiol. 173, 9–18.

Khan, N.A., Khan, M.I.R., Ferrante, A., Poor, P., 2017. Editorial: ethylene: a key regulatory molecule in plants. Front. Plant Sci. 8, 1782.

Kieber, J.J., Rothenberg, M., Roman, G., Feldmann, K.A., Ecker, J.R., 1993. CTR1, a negative regulator of the ethylene response pathway in Arabidopsis, encodes a member of the raf family of protein kinases. Cell. 12, 427–441.

Kim, J.H., Cho, H.T., Kende, H., 2000. α-Expansins in the semiaquatic ferns *Marsilea quadrifolia* and *Regnellidium diphyllum*: evolutionary aspects and physiological role in rachis elongation. Planta. 212, 85–92.

Kuroha, T., Nagai, K., Gamuyao, R., Wang, D.R., Furuta, T., Nakamori, M., et al., 2018. Ethylene-gibberellin signaling underlies adaptation of rice to periodic flooding. Science 361, 181–186.

Kurokawa, Y., Nagai, K., Huan, P.D., Shimazaki, K., Qu, H., Mori, Y., Toda, Y., Kuroha, T., Hayashi, N., Aiga, S., Itoh, J.I., Yoshimura, A., Sasaki-Sekimoto, Y., Ohta, H., Shimojima, M., Malik, A.I., Pedersen, O., Colmer, T.D., Ashikari, M., 2018. Rice leaf hydrophobicity and gas films are conferred by a wax synthesis gene (*LGF1*) and contribute to flood tolerance. New Phyto 218, 1558–1569.

Li, C.X., Wei, H., Geng, Y.H., Schneider, R., 2010. Effects of submergence on photosynthesis and growth of *Pterocarya stenoptera* (Chinese wingnut) seedlings in the recently-created three gorges reservoir region of China. Wetlands Ecol Manag. 18, 485–494.

Li, X.-J., Li, M., Zhou, Y., Hu, S., Hu, R., Chen, Y., Li, X.-B., 2015. Overexpression of cotton RAV1 gene in Arabidopsis confers transgenic plants high salinity and drought sensitivity. PLoS One 10, e0118056.

Licausi, F., Kosmacz, M., Weits, D.A., Giuntoli, B., Giorgi, F.M., Voesenek, L.A., Perata, P., van Dongen, J.T., 2011. Oxygen sensing in plants is mediated by an N-end rule pathway for protein destabilization. Nature 479, 419–422.

Liu, B., Rennenberg, H., Kreuzwieser, J., 2015. Hypoxia induces stem and leaf nitric oxide (NO) emission from poplar seedlings. Planta 241, 579–589.

Liu, M., Liu, X.X., He, X.L., Liu, L.J., Wu, H., Tang, C.X., Zhang, Y.S., Jin, C.W., 2017. Ethylene and nitric oxide interact to regulate the magnesium deficiency-induced root hair development in Arabidopsis. New Phytol. 213, 1242–1256.

Lorbiecke, R., Sauter, M., 1999. Adventitious root growth and cell-cycle induction in deepwater rice. Plant Physiol. 119, 21–29.

Lorenzo, P., Piqueras, R., Sánchez-Serrano, J.J., Solano, R., 2003. Ethylene response factor1 integrates signals from ethylene and jasmonate pathways in plant defense. Plant Cell 15, 165–178.

Lv, Y., Fu, S., Chen, S., Zhang, W., Qi, C., 2016. Ethylene response factor BnERF2-like (ERF2. 4) from Brassica *napus* L. Enhances submergence tolerance and alleviates oxidative damage caused by submergence in *Arabidopsis thaliana*. Crop J. 4, 199–211.

Ma, B., He, S.J., Duan, K.X., Yin, C.C., Chen, H., Yang, C., Zhang, W.K., 2013. Identification of rice ethylene-response mutants and characterization of MHZ7/OsEIN2 in distinct ethylene response and yield trait regulation. Mol. Plant 6, 1830–1848.

Mackill, D.J., Ismail, A.M., Singh, U.S., Labios, R.V., Paris, T.R., 2012. Development and rapid adoption of submergence-tolerant (Sub1) rice varieties. Advances Agron. 115, 303–356.

Magalhaes, J.R., Monte, D.C., Durzan, D., 2000. Nitric oxide and ethylene emission in *Arabidopsis thaliana*. Physiol. Mol. Biol. Plants 6, 117–127.

Mao, C., Wang, S., Jia, Q., Wu, P., 2006. OsEIL1, a rice homolog of the Arabidopsis EIN3 regulates the ethylene response as a positive component. Plant Mol. Biol. 61, 141–152.

Matías-Hernández, L., Aguilar-Jaramillo, A.E., Marín-González, E., Suárez-López, P., Pelaz, S., 2014. RAV genes: regulation of floral induction and beyond. Ann. Bot. 114, 1459–1470.

Mekhedov, S.L., Kende, H., 1996. Submergence enhances expression of a gene encoding 1-aminocyclopropane-1-carboxylate oxidase in deepwater rice. Plant Cell Physiol. 37, 531–537.

Mergemann, H., Sauter, M., 2000. Ethylene induces epidermal cell death at the site of adventitious root emergence in rice. Plant Physiol. 124, 609–614.

Metraux, J.-P., Kende, H., 1983. The role of ethylene in the growth response of submerged deepwater rice. Plant Physiol. 72 (441-), 446.

Mira, M.M., Hill, R.D., Stasolla, C., 2016. Phytoglobins improve hypoxic root growth by alleviating apical meristem cell death. Plant Physiol. 172, 2044–2056.

Mondal, S., Khan, M.I.R., Dixit, S., Cruz, P.C.S., Septiningsih, E.M., Ismail, A.M., 2020. Growth, productivity and grain quality of AG1 and AG2 QTLs introgression lines under flooding in direct-seeded rice system. Field Crops Res. 248 107713.

Müller, J.T., van Veen, H., Bartylla, M.M., Akman, M., Pedersen, O., Sun, P., Schuurink, R.C., Takeuchi, J., Todoroki, Y., Weig, A.R., Sasidharan, R., Mustroph, A., 2019. Keeping the shoot above water - submergence triggers antithetical growth responses in stems and petioles of watercress (*Nasturtium officinale*). New Phytol. https://doi.org/10.1111/nph.16350.

Musgrave, A., Walters, J., 1973. Ethylene-stimulated growth and auxin transport in *Ranunculus sceleratus* petioles. New Phytol. 72, 783–789.

Mustroph, A., Lee, S.C., Oosumi, T., Zanetti, M.E., Yang, H., Ma, K., Yaghoubi-Masihi, A., Fukao, T., Bailey-Serres, J., 2010. Cross-kingdom comparison of transcriptomic adjustments to low-oxygen stress highlights conserved and plant specific responses. Plant Physiol. 152 (1484-), 1500.

Nishiuchi, S., Yamauchi, T., Takahashi, H., Kotula, L., Nakazono, M., 2012. Mechanisms for coping with submergence and waterlogging in rice. Rice 5, 1.

Okishio, T., Sasayama, D., Hirano, T., Akimoto, M., Itoh, K., Azuma, T., 2014. Ethylene is not involved in adaptive responses to flooding in the amazonian wild rice species *Oryza grandiglumis*. J. Plant Physiol. 174, 49–54.

Parlanti, S., Kudahettige, N.P., Lombardi, L., Mensuali-Sodi, A., Alpi, A., Perata, P., Pucciariello, C., 2011. Distinct mechanisms for aerenchyma formation in leaf sheaths of rice genotypes displaying a quiescence or escape strategy for flooding tolerance. Ann. Bot. 107, 1335–1343.

Pedersen, O., Rich, S.M., Colmer, T.D., 2009. Surviving floods: leaf gas films improve O_2 and CO_2 exchange, root aeration, and growth of completely submerged rice. Plant J. 58, 147–156.

Pellegrini, E., Konnerup, D., Winkel, A., Casolo, V., Pedersen, O., 2017. Internal tissue aeration in two halophytes of the mediterranean region, during partial and complete submergence. Funct. Plant Biol. 44, 867–876.

Pen˜a-Castro, J.M., van Zanten, M., Lee, S.C., Patel, M.R., Voesenek, L.A., Fukao, T., Bailey-Serres, J., 2011. Expression of rice SUB1A and SUB1C transcription factors in Arabidopsis uncovers flowering inhibition as a submergence tolerance mechanism. Plant J. 67, 434–446.

Perata, P., 2019. Ethylene signaling controls fast oxygen sensing in plants. Trends Plant Sci. 25, 3–6.

Rajhi, I., Yamauchi, T., Takahashi, H., Nishiuchi, S., Shiono, K., Watanabe, R., Nakazono, M., 2011. Identification of genes expressed in maize root cortical cells during lysigenous aerenchyma formation using laser microdissection and microarray analyses. New Phytol. 190, 351–368.

Raskin, I., Kende, H., 1984. Regulation of growth in stem sections of deep-water rice. Planta 160, 66–72.

Rijnders, J.G.H.M., Yang, Y.Y., Kamiya, Y., Takahashi, N., Barendse, G.W., Blom, C.W., Voesenek, L.A.C.J., 1997. Ethylene enhances gibberellin levels and petiole sensitivity in flooding-tolerant *Rumex palustris* but not in flooding-intolerant R. Acetosa. Planta. 203, 20–25.

Rose, J.K.C., Cosgrove, D.J., Albersheim, P., Darvill, A.G., Bennett, A.B., 2000. Detection of expansin proteins and activity during tomato fruit ontogeny. Plant Physiol. 123, 1583–1592.

Rzewuski, G., Sauter, M., 2008. Ethylene biosynthesis and signaling in rice. Plant Sci. 175, 32–42.

Saab, I.N., Sachs, M.M., 1996. A flooding-induced xyloglucan endo transglycosylase homolog in maize is responsive to ethylene and associated with aerenchyma. Plant Physiol. 112, 385–391.

Saika, H., Okamoto, M., Miyoshi, K., Kushiro, T., Shinoda, S., Jikumaru, Y., Arimura, S.I., 2007. Ethylene promotes submergence-induced expression of OsABA8ox1, a gene that encodes ABA 8′-hydroxylase in rice. Plant Cell Physiol. 48, 287–298.

Sarkar, R.K., Bhattacharjee, B., 2011. Rice genotypes with SUB1 QTL differ in submergence tolerance, elongation ability during submergence and re-generation growth at re-emergence. Rice. 5, 1.

Sasidharan, R., Voesenek, L.A.C.J., 2015. Ethylene-mediated acclimations to flooding stress. Plant Physiol. 169, 3–12.

Sasidharan, R., Hartman, S., Liu, Z., Martopawiro, S., Sajeev, N., van Veen, H., Yeung, E., Voesenek, L.A.C.J., 2018. Signal dynamics and interactions during flooding stress. Plant Physiol. 176, 1106–1117.

Satoh, M., Tokaji, Y., Nagano, A.J., Hara-Nishimura, I., Hayashi, M., Nishimura, M., Ohta, H., Masuda, S., 2013. Arabidopsis mutants affecting oxylipin signaling in photo-oxidative stress responses. Plant Physiol. Biochem. 81, 90–95.

Sauter, M., 2000. Rice in deep water: how to take heed against a sea of troubles. Naturwissenschaften 87, 289–303.

Schmitz, A.J., Folsom, J.J., Jikamaru, Y., Ronald, P., Walia, H., 2013. *SUB1A*-mediated submergence tolerance response in rice involves differential regulation of the brassinosteroid pathway. New Phytol. 198, 1060–1070.

Septiningsih, E.M., Pamplona, A.M., Sanchez, D.L., Neeraja, C.N., Vergara, G.V., Heuer, S., Mackill, D.J., 2009. Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. Ann. Bot. 103, 151–160.

Setter, T.L., Waters, I., Wallace, I., Bhekasut, P., Greenway, H., 1989. Submergence of rice. I. Growth and photosynthetic response to co2 enrichment of floodwater. Funct. Plant Biol. 16, 251–263.

Sharoni, A.M., Nuruzzaman, M., Satoh, K., Shimizu, T., Kondoh, H., Sasaya, T., Choi, I.-R., Omura, T., Kikuchi, S., 2011. Gene structures, classification and expression models of the AP2/EREBP transcription factor family in rice. Plant Cell Physiol. 52, 344–360.

Shen, X., Wang, Z., Song, X., Xu, J., Jiang, C., Zhao, Y., Ma, C., Zhang, H., 2014. Transcriptomic profiling revealed an important role of cell wall remodeling and ethylene signaling pathway during salt acclimation in Arabidopsis. Plant Mol. Biol. 86, 303–317.

Singh, P., Sinha, A.K., 2016. A positive feedback loop governed by SUB1A1 interaction with MITOGEN-ACTIVATED PROTEIN KINASE3 imparts submergence tolerance in rice. Plant Cell 28, 1127–1143.

Singh, S., Mackill, D.J., Ismail, A.M., 2009. Responses of SUB1 rice introgression lines to submergence in the field: yield and grain quality. Field Crops Res. 113, 12–23.

Singh, N., Dang, T.T., Vergara, G.V., Pandey, D.M., Sanchez, D., Neeraja, C.N., Mackill, D.J., 2010. Molecular marker survey and expression analyses of the rice submergence-tolerance gene SUB1A. Theor. Appl. Genet. 121, 1441–1453.

Singh, S., Mackill, D.J., Ismail, A.M., 2014. Physiological basis of tolerance to complete submergence in rice involves genetic factors in addition to the SUB1 gene. AoB Plants 6, plu060.

Stearns, J.C., Glick, B.R., 2003. Transgenic plants with altered ethylene biosynthesis or perception. Biotech Adv 21, 193–210.

Steffens, B., Rasmussen, A., 2016. The physiology of adventitious roots. Plant Physiol. 170, 603–617.

Steffens, B., Sauter, M., 2005. Epidermal cell death in rice is regulated by ethylene, gibberellin, and abscisic acid. Plant Physiol. 139, 713–721.

Steffens, B., Sauter, M., 2009. Epidermal cell death in rice is confined to cells with a distinct molecular identity and is mediated by ethylene and H_2O_2 through an autoamplified signal pathway. Plant Cell 21, 184–196.

Steffens, B., Wang, J., Sauter, M., 2006. Interactions between ethylene, gibberellin and abscisic acid regulate emergence and growth rate of adventitious roots in deepwater rice. Planta 223, 604–612.

Steffens, B., Kovalev, A., Gorb, S.N., Sauter, M., 2012. Emerging roots alter epidermal cell fate through mechanical and reactive oxygen species signaling. Plant Cell 24, 3296–3306.

Steffens, B., Steffen-Heins, A., Sauter, M., 2013. Reactive oxygen species mediate growth and death in submerged plants. Front. Plant Sci. 4, 179.

Summers, J.E., Voesenek, L.A.C.J., Blom, C.W.P.M., Lewis, M.J., Jackson, M.B., 1996. *Potamogeton pectinatus* is constitutively incapable of synthesizing ethylene and lacks 1-aminocyclopropane-1-carboxylic acid oxidase. Plant Physiol. 111, 901–908.

Swaminathan, K., Peterson, K., Jack, T., 2008. The plant B3 superfamily. Trends Plant Sci. 13, 647–655.

Tamang, B.G., Fukao, T., 2015. Plant adaptation to multiple stresses during submergence and following desubmergence. Int. J. Mol. Sci. 16, 30164–30180.

Thao, N.P., Khan, M.I.R., Thu, N.B.A., Hoang, X.L.T., Asgher, M., Khan, N.A., Tran, L.S.-P., 2015. Role of ethylene and its cross talk with other signaling molecules in plant responses to heavy metal stress. Plant Physiol. 169, 73–84.

Van Bodegom, P.M., Sorrell, B.K., Oosthoek, A., Bakker, C., Aerts, R., 2008. Separating the effects of partial submergence and soil oxygen demand on plant physiology. Ecology 89, 193–204.

Van de Poel, B., Smet, D., Van Der Straeten, D., 2015. Ethylene and hormonal cross talk in vegetative growth and development. Plant Physiol. 169, 61–72.

van der Straeten, D., Zhou, Z., Prinsen, E., van Onckelen, H.A., van Montagu, M.C., 2001.). A comparative molecular-physiological study of submergence response in lowland and deepwater rice. Plant Physiol. 125, 955–968.

Vidoz, M.L., Mignolli, F., Aispuru, H.T., Mroginski, L.A., 2016. Rapid formation of adventitious roots and partial ethylene sensitivity result in faster adaptation to flooding in the aerial roots (aer) mutant of tomato. Sci. Hortic. Amst 201, 130–139.

Visser, E.J., Cohen, J.D., Barendse, G.W., Blom, C.W., Voesenek, L.A., 1996. An ethylene-mediated increase in sensitivity to auxin induces adventitious root formation in flooded Rumex palustris Sm. Plant Physiol. 112, 1687–1692.

Voesenek, L.A.C.J., Bailey-Serres, J., 2015. Flood adaptive traits and processes: an overview. New Phyto 206, 57–73.

Voesenek, L.A.C.J., Blom, C.W.P.M., 1999. Stimulated shoot elongation: a mechanism of semiaquatic plants to avoid submergence stress. In: Lerner, H.R. (Ed.), In Plant Responses to Environmental Stress: From Phytohormones to Genome Reorganization. Marcel Dekker, New York, pp. 431–448.

Voesenek, L.A.C.J., Sasidharan, R., 2013. Ethylene- and oxygen signalling drive plant survival during flooding. Plant Bio. 15, 426–435.

Voesenek, L.A.C.J., Benschop, J.J., Bou, J., Cox, M.C.H., Groeneveld, H.W., Millenaar, F.F., Peeters, A.J.M., 2003. Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot Rumex palustris. Ann. Bot. 91, 205–211.

Voesenek, L.A.C.J., Colmer, T.D., Pierik, R., Millenaar, F.F., Peeters, A.J.M., 2006. How plants cope with complete submergence. New Phytol. 170, 213–226.

Voesenek, L.A.C.J., Pierik, R., Sasidharan, R., 2015. Plant life without ethylene. Trends Plant Sci. 20, 783–786.

Vogel, M.O., Gomez-Perez, D., Probst, N., Dietz, K.J., 2012. Combinatorial signal integration by APETALA2/Ethylene response factor (ERF)-transcription factors and the involvement of AP2-2 in starvation response. Int. J. Mol. Sci. 13, 5933–5951.

Vreeburg, R.A., Benschop, J.J., Peeters, A.J., Colmer, T.D., Ammerlaan, A.H., Staal, M., Elzenga, T.M., Staals, R.H.J., Darley, C.P., McQueen-Mason, S.J., Voesenek, L.A.C.J., 2005. Ethylene regulates fast apoplastic acidification and expansin A transcription during submergence-induced petiole elongation in *Rumex palustris*. Plant J. 43, 597–610.

Vriezen, W.H., De Graaf, B., Mariani, C., Voesenek, L.A.C.J., 2000. Submergence induces expansin gene expression in flooding-tolerant *Rumex palustris* and not in flooding-intolerant R. Acetosa. Planta 210, 956–963.

Wang, X., Ma, Q., Wang, R., Wang, P., Liu, Y., Mao, T., 2020. Submergence stress-induced hypocotyl elongation through ethylene signaling-mediated regulation of cortical microtubules in Arabidopsis. J. Exp. Bot. 71, 1067–1077.

Watanabe, H., Saigusa, M., Hase, S., Hayakawa, T., Satoh, S., 2004. Cloning of a cDNA encoding an ETR2-like protein (Os-ERL1) from deep water rice (*Oryza sativa* L.) and increase in its mRNA level by submergence, ethylene, and gibberellin treatments. J. Exp. Bot. 55, 1145–1148.

Winkel, A., Colmer, T.D., Ismail, A.M., Pedersen, O., 2013.). Internal aeration of paddy field rice (*Oryza sativa* L.) during complete submergence – importance of light and floodwater O_2. New Phytol. 197, 1193–1203.

Winkel, A., Pedersen, O., Ella, E., Ismail, A.M., Colmer, T.D., 2014. Gas film retention and underwater photosynthesis during field submergence of four contrasting rice genotypes. J. Exp. Bot. 65, 3225–3233.

Winkel, A., Visser, E.J.W., Colmer, T.D., Brodersen, K.P., Voesenek, L.A.C.J., Sand-Jensen, K., Pedersen, O., 2016. Leaf gas films, underwater photosynthesis and plant species distributions in a flood gradient. Plant, Cell Env 39, 1537–1548.

Woo, H.R., Kim, J.H., Kim, J., Kim, J., Lee, U., Song, I.-J., Kim, J.-H., Lee, H.Y., Nam, H.G., Lim, P.O., 2010. The RAV1 transcription factor positively regulates leaf senescence in Arabidopsis. J. Exp. Bot. 61, 3947–3957.

Wu, Y.S., Yang, C.Y., 2016. Physiological responses and expression profile of NADPH oxidase in rice (*Oryza sativa*) seedlings under different levels of submergence. Rice 9, 1.

Wu, H., Chen, H., Zhang, Y., Zhu, D., Xiang, J., 2019. Effects of 1-aminocyclopropane-1-carboxylate and paclobutrazol on the endogenous hormones of two contrasting rice varieties under submergence stress. Plant Growth Regul. 87, 109–121.

Wuriyanghan, H., Zhang, B., Cao, W.H., Ma, B., Lei, G., Liu, Y.F., Wei, W., Wu, H.-J., Chen, L.-J., Chen, H.-W., Cao, Y.-R., He, S.-J., Zhang, W.-K., Wang, X.-J., Chen, S.-Y., Zhang, J.-S., 2009. The ethylene receptor ETR2 delays floral transition and affects starch accumulation in rice. Plant Cell 21, 1473–1494.

Xie, L.J., Chen, Q.F., Chen, M.X., Yu, L.J., Huang, L., Chen, L., Wang, F.Z., Xia, F.N., Zhu, T.R., Wu, J.X., et al., 2015. Unsaturation of very-long-chain ceramides protects plant from hypoxia-induced damages by modulating ethylene signaling in Arabidopsis. PLoS Genet. 11, e1005143.

Xu, K.N., Mackill, D.J., 1996. A major locus for submergence tolerance mapped on rice chromosome 9. Mol. Breed. 2, 219–224.

Xu, K., Xu, X., Fukao, T., Canlas, P., Maghirang-Rodriguez, R., Heuer, S., Ismail, A.M., Bailey-Serres, J., Ronald, P.C., Mackill, D.J., 2006. Sub1A is an ethylene response factor-like gene that confers submergence tolerance to rice. Nature 442, 705–708.

Yamasaki, K., Kigawa, T., Inoue, M., Tateno, M., Yamasaki, T., Yabuki, T., Aoki, M., Seki, E., Matsuda, T., Tomo, Y., Hayami, N., Terada, T., Shirouzu, M., Osanai, T., Tanaka, A., Seki, M., Shinozaki, K., Yokoyama, S., 2004. Solution structure of the B3 DNA binding domain of the Arabidopsis cold-responsive transcription factor RAV1. Plant Cell 16, 3448–3459.

Yamauchi, T., Watanabe, K., Fukazawa, A., Mori, H., Abe, F., Kawaguchi, K., Oyanagi, A., Nakazono, M., 2014. Ethylene and reactive oxygen species are involved in root aerenchyma formation and adaptation of wheat seedlings to oxygen-deficient conditions. J. Exp. Bot. 65, 261–273.

Yamauchi, T., Tanaka, A., Mori, H., Takamure, I., Kato, K., Nakazono, M., 2016. Ethylene-dependent aerenchyma formation in adventitious roots is regulated differently in rice and maize. Plant Cell Environ. 39, 2145–2157.

Yamauchi, T., Yoshioka, M., Fukazawa, A., Mori, H., Nishizawa, N.K., Tsutsumi, N., Yoshioka, H., Nakazono, M., 2017. An NADPH oxidase RBOH functions in rice roots during lysigenous aerenchyma formation under oxygen-deficient conditions. Plant Cell 29, 775–790.

Yamauchi, T., Tanaka, A., Tsutsumi, N., Inukai, Y., Nakazono, M., 2020. A role for auxin in ethylene-dependent inducible aerenchyma formation in rice roots. Plants 9, 610.

Yang, H.J., Shen, H., Chen, L., Xing, Y.Y., Wang, Z.Y., Zhang, J.L., Hong, M.-M., 2002. The OsEBP-89 gene of rice encodes a putative EREBP transcription factor and is temporally expressed in developing endosperm and intercalary meristem. Plant Mol. Biol. 50, 379–391.

Yang, C., Ma, B., He, S.J., Xiong, Q., Duan, K.X., Yin, C.C., Chen, H., Lu, X., Chen, S.Y., Zhang, J.S., 2015. MAOHUZI6/ETHYLENE INSENSITIVE3-LIKE1 and ETHYLENE INSENSITIVE3-LIKE2 regulate ethylene response of roots and coleoptiles and negatively affect salt tolerance in rice. Plant Physiol. 169, 148–165.

Yeung, E., van Veen, H., Vashisht, D., Sobral Paiva, A.L., Hummel, M., Rankenberg, T., Steffens, B., Steffen-Heins, A., Sauter, M., de Vries, M., et al., 2018. A stress recovery signaling network for enhanced flooding tolerance in *Arabidopsis thaliana*. PNAS 115, E6085–E6094.

Yeung, E., Bailey-Serres, J., Sasidharan, R., 2019. After the deluge: plant revival post flooding. Trends Plant Sci. 24, 443–454.

Yin, D., Chen, S., Chen, F., Jiang, J., 2013.). Ethylene promotes induction of aerenchyma formation and ethanolic fermentation in waterlogged roots of *Dendranthema* spp. Mol. Biol. Rep. 40, 4581–4590.

Yu, K.O.N.G., Zhong, W.A.N.G., Juan, C.H.E.N., Pan, X.T., Liu, D.T., Zhang, E.J., 2009. Effects of ethephon on aerenchyma formation in rice roots. Rice Sci. 16, 210–216.

Yukiyoshi, K., Karahara, I., 2014. Role of ethylene signalling in the formation of constitutive aerenchyma in primary roots of rice. AoB Plants 6, plu043.

Zarembinski, T.I., Theologis, A., 1997. Expression characteristics of OS-ACS1 and OS-ACS2, two members of the 1-aminocyclopropane-1-carboxylate synthase gene family in rice (*Oryza sativa* L. Cv. Habiganj Aman II) during partial submergence. Plant Mol. Biol. 33, 71–77.

Zhou, Z., Engler, J.A., Rouan, D., Michiels, F., van Montagu, M., van der Straeten, D., 2002. Tissue localization of a submergence-induced 1-aminocyclopropane-1-carboxylic acid synthase in rice. Plant Physiol. 129, 72–84.