

## Review

# An updated overview of the physiological and molecular responses of rice to anoxia

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## 1. Abstract

Waterlogging or flooding in agricultural soil constructs a complex abiotic stress-web in crop plants throughout the lowland agricultural system. In rice, a staple grain crop in the world, submergence creates a long-term and recurrent problem for crops withstanding and their succeeding productivity. Therefore, to restore a satisfactory yield instead of a failure of crop in such submerged areas, the analysis of plants' responses is important. Such analysis will facilitate research about the entity components of plants responses to anoxia or submergence. For example, the development of cellular and molecular cascade in gene expression of ROS signaling and its subsequent responses may lead to either tolerance or susceptibility in plants. Interplay of plant growth regulators [e.g., ethylene (ET), abscisic acid (ABA), gibberellic acid (GA) etc.] is the well-recognized residues in the coordination of signaling, its transmission through cellular network, and finally, mod-

ulation of gene expression are the keys to such tolerance. Nucleotide elements that are specifically sensitive to ethylene have been rescued from land-races of aus-type group of rice (*Oryza sativa*) and those are considered as the prime determinants for tolerance against anoxia. In this comprehensive text, we tried to accommodate and revise the fundamental and pivotal mechanisms of submergence stress at different angles of physiological and cellular responses of plants. These have also been reviewed for modern state of art techniques deciphering the molecular rejoinders like microRNA, protein-protein interaction, feedback regulation of expression, sugar sensing, amplification of elicitor's responses and others. Finally, strategies including physiological selection, metabolic engineering, marker assisted selection, genetical manipulation, interspecific hybridization are involved in developing stress resilience and plants' architecture to support sustainable agriculture under lowland systems.

## 2. Introduction

Climate change has been a pre-historic event that appears in different scenarios with facets to affect the vegetation. Time immemorial such a change of climate has been more accurately vulnerable to agriculture through a failure of crops survival, growth and productivity. As a result, yield loss occurs which leads to insecurity of food supply to the society. Thus, agriculturists and scientists worldwide face challenges to ensure proper inputs (e.g., soil, water, temperature, air and other edaphic factors) for crop cultivation [1]. These constraints of abiotic factors are technically called stressors and to overcome these stressors there are certain measures, policies and technical acts adapted so far besides the development of stress resistant plant types by the plant breeders. Adaptation of the strategies in updating and improving the agricultural land is based on nutrient cycling, decontamination, water availability, gaseous enrichment etc. [2]. So, it would be a positive thrust to select tolerant genotypes to accustom to such a climate change. Of course, most of the selected plants for stress tolerance may not necessarily be linked to adequate productivity. To combine those two traits together the research and technology rely on primarily, to dissect out the mechanism of tolerance. On the other hand, another module of research aims to find out the traditional cultivars or landraces with low yield but wider ranges of adaptability [3]. The analysis, even at the molecular level through phenological, physiological, cellular pathways, for regulation and induction of tolerance are the enriched insights. This is also to exercise for any genotype and its retrieval of traits that might have been lost in course of evolution.

Significant loss of genetic diversity including stress responses of different cultivars might possess some transferable traits to support tolerance to other related species in question. This approach essentially includes a mass selection or trial of wider ranges of genotypes either to adopt to a particular, or multi-stress factor(s). This is followed by understanding the mechanism of stress reactions as well as its underlying regulation mechanism [4]. The latter is the most finely detected to locate for specific sequences, heritable as well as linked to one or more quantitative trait locus (QTL). The later may satisfy the integrated breeding program updated with high yielding cultivars and that conceives the marker-assisted selection in a breeding program [5].

Among the different abiotic stresses, abundance of water, technically referred to flooding constitutes a complex situation before crop growth and development. Flooding causes either partial waterlogging or complete inundation. When the water level covers only roots or half of the aerial trunk, the situation is termed as waterlogging [6]. Submergence refers to when it completely sunk the shoot of the plants for significant days with varying depths of water. This essentially ensures the depletion of oxygen to

the plants below its optimum level for growth. In case of submergence; this also induces other abiotic stressors like moisture deficits, an abundance of dissolved ions, limited irradiance and biotic stressors (pathogen, insect etc.) too. Even after recede of excess water, an oxidative exposure along with remobilization of reserved materials also hampered plant sustainability [7]. Stagnation of water in the different ecological niche would also dictate the compositional species diversity, dominance, specific traits to such environment and finally declaration of ecotypes. The impetus of research in the domain of submergence stress additionally allows de-folds plants reaction to depleted gases with special reference to partial oxygen pressure. An anoxic or hypoxic condition is manifested in plants with other factors of stress responses directly or indirectly for lowland submerged rice cultivation. Plants retort the submergence stress and allied events through changes of multi-level gene expression. These include changes in epigenetic manifestation to transcriptomics operation followed by translational modification. So, breeding for tolerance aspects under such oxygen deficit condition ought to communicate every method in the analysis of plants' come back including phenomics, metabolomics, proteomics, genomics etc. [8]. Still, this chapter may encompass the updates of proceedings regarding submergence tolerance with other advanced content of signaling cascade, regulation with microRNA, the contribution of polymorphism of proteins, specific environmental elicitation etc. This would also cover the approaches for biotechnological interventions, modern state of art and strategies in developing specific crop ideotypes against anoxic reaction as well as to modulate in favor of sustenance. The insights are also expected to have the identification of heritable determinants in lieu of climate resilient crops under changing global environment.

## 3. Approved strategies by plants: To avoid submergence or to adopt

This has been well referred that submergence *vis-a-vis* anoxia can induce significant changes in gene expression. Collectively submerged tissues are coordinated with metabolic and physiological manifestation predominantly to meet the fermentative mode of energy-yielding metabolism [9]. In the case of submergence with special reference to rice plants two general strategies of tolerance are required: escape and quiescence (Fig. 1). For both the cases, it is the interplay of growth substances to dominate any of those and complement respective alteration of plants responses. The key for these two strategies is primarily based on the management of oxygen deficiency under such ecological niche either to avoid or adapt to the anoxia. Physiologically flooded plants hardly having photosynthetic activities under water is lagged behind optimum, even minimum oxygen tension to survive through growth respiration. Only aquatic or semi-aquatic plant

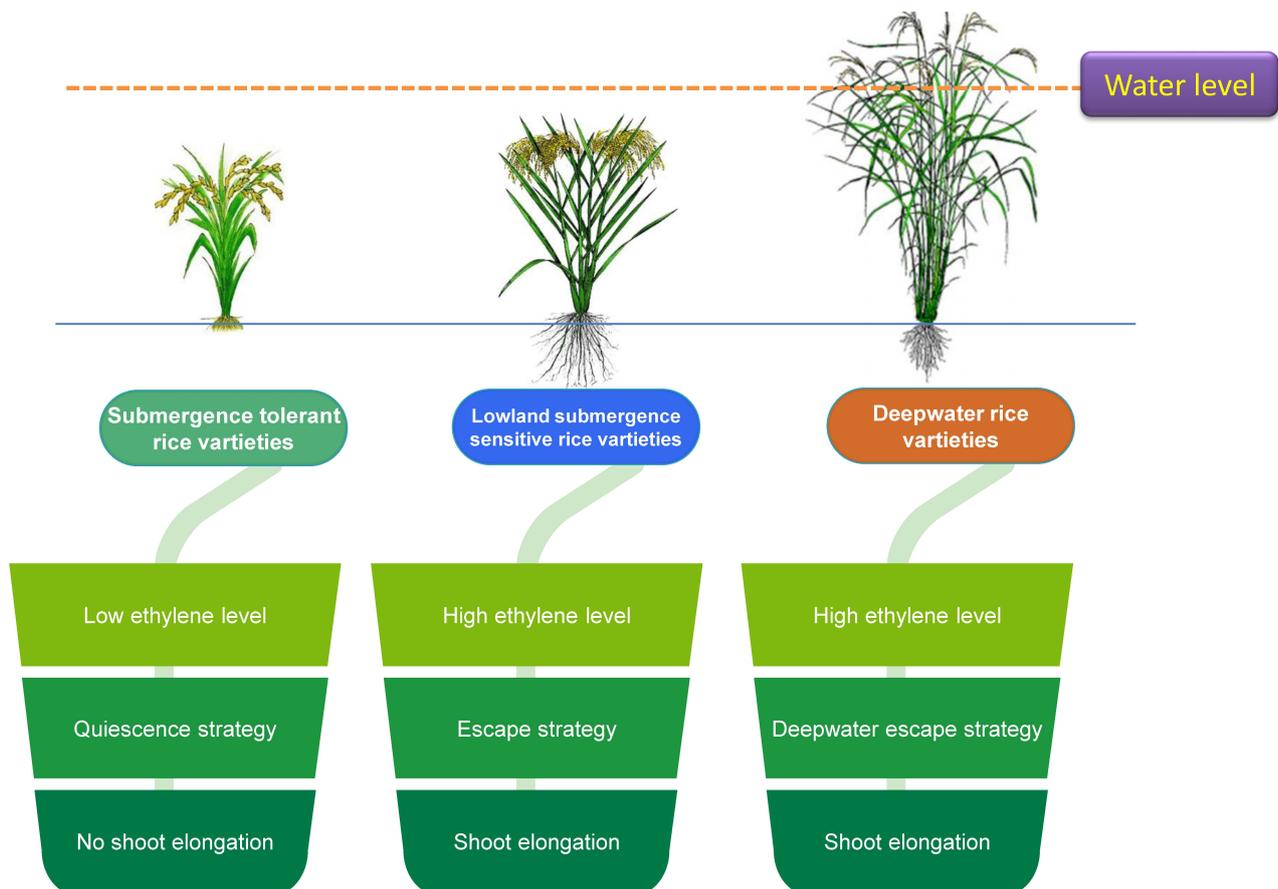


Fig. 1. Escape and quiescence strategies in submergence tolerant and intolerant rice varieties.

species can tolerate anoxia accordingly and grow and reproduce under water. In contrast, non aquatic species may also thrive under such conditions but for a very short span of exposure and thereafter exerts to be overgrow the water level by increasing their linear growth. For example, tall *indica* landraces of rice have been in the practice of this strategy where a significant intermodal and leaf sheath elongation occur to pursue escape strategy [10]. This later may be granted as an avoidance phenomenon with some improved morphological and anatomical features facilitating the exchange of oxygen and other gases with that niche. The development of aerenchyma at the sub-cellular level by coalesces of few cortical thin-walled tissues. Besides, at the morphological level the shoot-borne adventitious roots under water are other inducible characters adhered to this strategy, mostly found in rice as well as other species [11]. In some special adaptations, the aerenchyma bound tissues have distinct layers with suberin to check the radial depletion of oxygen or radial oxygen loss (ROL). Few plant species are good consumers of a huge amount of carbohydrates to support the available substrate for elongating cells. Specific gene expression with starch hydrolyzing enzymes may be a factor to put forth the escape strategy.

There are few plant species including rice landraces which are efficient survivors under depleted oxygen

concentration particularly for their dwarf nature. This adaptation is exclusively based on reduced or suppressed growth under water to minimize the loss of energy for living tissues and thereby adopt fermentative metabolism [12]. The limitation of respiration under low oxygen pressure is exclusively glycolytic following fermentative ATP generation which becomes the sole source of tissue viability. However, sensitive species despite their ability to ferment may not survive due to the presence of toxic products for a considerable period. Therefore, plants are forced to suppress the growth in the internodes by the up/downregulation of few growth regulators like ethylene (ET), gibberellic acid (GA), abscisic (ABA) etc. The tolerant genotypes can exercise the quiescence strategy exclusively by downregulation of GA metabolism through interference with ET. At metabolic level under oxygen deficient condition, the precursor of ET, 1-amino 1-propane carboxylic acid (ACC) may accumulate and impose negative feedback to the GA biosynthesis. This sets a number of genes to distribute in the number of QTL, initially derived from semi-tall *Aus* type landraces like FR-13A and the loci is recognized as *sub1* [13]. Physically the locus size covers around 200 kb of which a significant variation (about 40–65%) occurs for two subspecies of rice viz. *indica* and *japonica* according to their tolerant and susceptible responses. This QTL is exclusively seated

on chromosome No.19 of the FR-13A. Basically, the sequence of the locus is responsible to encode three transcription factors (*sub1A*, *sub1B* and *sub1C*) for genes sensitive to ET (C<sub>2</sub>H<sub>4</sub>). Transcription factors encoded by this sequence belong to B2 subgroup of ethylene-responsive factors (ERF) or ethylene response binding proteins (ERBPs) or apetala (*AP2*). The activity of *sub1A* and *sub1C* inductions is dependent on submergence and *vis-a-vis* upon de-submergence [14]. In few cases *sub1A* can down-regulate *sub1C*, whereas *sub1B* is less upregulated by submergence, thus establishing the predominant role of *sub1A*. So, ET must be the key in submergence tolerance with its quiescence strategies. Submergence tolerant rice genotypes are often characterized by an abundance of ET accumulation when grown under complete submergence condition [15]. This is accompanied by an increase of fermentation mechanism and shifting the plants towards the anaerobic mode of respiration linking to repression of genes for elongation of the internodal tissues and carbohydrate metabolism. *sub1A* in turn is also responsible for feedback regulation of ET generation by blocking the key gene(s) biosynthesis. This has been well-examined with the transformation of *sub1A* into susceptible rice landraces showing wider ranges of tolerance in terms of subdued growth and access to fermentation metabolism. Moreover, the depletion of starch by GA-induced hydrolytic activity in culm as well as mobilization of sugars was also regulated on the successful expression of the genes. Alternatively, expression of ET-dependent genes increased the activities of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) demonstrating the heritable cellular responses under induced submergence [16]. Therefore, all this is subjected to the availability of *sub1A* based ET governing to forward the quiescence strategies in intolerant genotypes exposed to submergence. Another growth regulator GA appears to be involved in a more complicated manner in the regulation of *sub1C*. The latter may control the *RAmy3D* which causes a breakdown of starch to glucose even under submergence. Meanwhile, in tolerant genotype *sub1A* negatively control the activity of *RAmy3D*. Maybe the regulatory elements of the *RAmy3D* lack the GA response elements (GARE) and thereby direct involvement of GA is annulled [17]. It is also expected that the intolerant genotypes lacking *sub1A* is deficient insoluble sugars and upregulation of *RAmy3D* may provide the energy by activating GA-induced hydrolysis of the carbohydrates. Typical deepwater rice under submergence is dependent on another ERF called *SNORKEL*<sup>1</sup> and 2 (*SK1* and *SK2*). In fact, to suppress the internodal elongation *sub1A* may increase an inhibitor of GA called *SLENDER RICE LIKE* (*SLRL1* and *SLR2*).

#### 4. Ethylene: The key player for submergence tolerance in rice

Rice, a common semi-aquatic plant has three distinct ecotypes in habitat in relation to water level. In rice fallows, partial submergence or stagnation of water is considered as normal for its growth and development. Despite drastic fall in diffusion rate of O<sub>2</sub>, CO<sub>2</sub> and other gases as well as inhibition of gas exchange between tissues and environment, rice genotypes become able to survive with subdued photosynthesis rate and respiration by genetic plasticity. Still, three distinct habitats are experienced by rice, lowland, deep water and upland ecological niche according to the depth of water in fallows. Besides the upland situation, rice plants are exclusively based on involvement as well as interference of ET on their survival under inundated condition either by escape or quiescence strategies [18]. For both escape and quiescence strategies, the promotion and suppression of shoot growths are required which are influenced by ET metabolism. Intercellular ET concentration is increased (by almost 100-fold than ambient condition) with other physiological processes when rice plant is subjected to submergences as reported in deepwater rice [19]. A dramatic increase in ET concentration is noted in submergence tolerant rice genotypes when exposed to submergence. In fact, the hypoxic condition is more favored by ethylene biosynthesis under submerged tissues. The key gene for ET biosynthesis is the ACC synthase (ACS) with few isoforms transcripts that becomes abundant in roots and culm of rice seedling under submergence condition. With *in situ* hybridization techniques, it was observed that ACS transcript is more abundant in vascular tissues where specific cells are dependent on ET for both cell division and elongation. ACC oxidase (ACO) is another enzyme that causes the conversion of ACC to ET. Parallel to ACC, significant upregulation of ACO in internode or leaf sheath in submerged plants was also recorded [20]. The boost of ACO activity undoubtedly reveals the ability to develop adventitious roots along with a continued supply of ET in tolerant rice genotypes during submergence. For the inter-nodal elongation other hormones like GA and ABA intricate to the ET metabolism in the inter-nodal section and has distinct steps forward to adventitious root formation like death of the epidermal cells at the site of root emergence following growth of the adventitious roots over there. Ethylene-mediated such responses are auxiliary facilitated by GA, but ABA becomes a negative regulator to ET. In fact, ET is the regulator in balancing the ratio of GA to ABA; this is also supported for shoot elongation in deepwater rice where ET along with GA may contribute but the process is regulated negatively by ABA [21].

It is well admitted that ET signaling on cell surface and plasma membrane is triggered on its binding to specific receptor proteins called ET receptors [22]. A number of ET receptors (ETR1) have been identified from

*Arabidopsis* and their molecular organization, functioning and induction of different genes were properly elucidated [23]. Still, more updated information regarding different ETR1, ETR2 and their commonness or variability, interacting proteins regulation and evolutionary trends through higher plants are yet to be scrutinized and understood. The different cross-talks between ET signaling and other plant hormones particularly, ABA, GA and few elicitors like jasmonic acid (JA) are integrated for molecular insights of ET functioning under submergence or any other inducing anoxia. Identification and characterization from different mutants where triple response is lacked and could also isolate the responsible genes and their epistatic interaction in ET signaling pathways [24]. Binding with ET and ETR1 could regulate; however, negatively the developmental role of ET in plants as well as stress response. In absence of ET those receptor proteins interact to ETR1 at a constitutive triple response (CTR) that inhibits ET signaling [25]. The direct interaction between receptor proteins and ETR1 in downstream restricts the binding with ET insensitive 2 (EIN2) [26]. EIN2 is dissociated by some F-box proteins and thereby, ET signaling is inhibited. ET can change the confirmation of receptor complex and those results to inactivate CTR1. This even allows the binding of kinases domain to EIN2. On downstream, phosphorylated form of EIN2 undergoes hydrolysis to dissociate its C-terminal ends and enters into nucleus. The fragment of C-terminal ends in the nucleus functions to replace EIN3 binding mRNA to translate outside the nucleus [27]. This activates the other transcription factors EIN3-like 1 (EIL1). On the same time in the nucleus the C-terminal of EIN2 interacts with other transcription factors: EIN2 nuclear-associated protein1 (ENAP1) that regulates histone acetylation of some histone kinases (H3K14, H3K23) and as a whole promotes the ET sensitive genes [28]. ET signaling has been more updated with reference to submergence stress where anoxia may trigger the various chemical modifications like phosphorylation/dephosphorylation, acetylation and others complex networks to induce and amplify ET signaling in downstream. As for example CTR1 is able to interact many ET receptors in differential affinities. The binding of ET to those receptors brings the conformational changes that would disintegrate the receptor-CTR1 interaction to set free the CTR1 [29]. The released CTR1 is the key to activate ET responses. Still, functional mechanism of EIN2 also raises the question like what function of transmembrane domain of EIN2 and what mechanism for entry of C-terminal domain from EIN2 into nucleus is responsible. Additionally, a complex web on transcriptional, post transcriptional/translational and other epigenetic regulation are well studied for plant development with ET. Still, there are no significant reports on epigenetic control of ET signaling. The function of ETR1 signaling from loss-of-function mutant has included the intervention of ABA [30]. ETR1 has the analogy to replace the ABA-induced

ETR1 transcription, and on the other hand ETR2 down regulates the ABA induction upon ETR1 and EIN4 gene expression. Other growth regulators like chemical elicitors (JA, salicylic acid) have relative effectiveness on signaling through EIN3. SA activates NPR1 (Nonexpressor of pathogenesis-related genes 1) which physically binds with EIN3 that as a whole curtails the binding to its specific promoters [31]. This undoubtedly suggests that the ET signaling for development and stress responses is not simplified at all rather may encompass other signaling residues where EIN3, EIL1 are important. All these researches invariably indicate the existence of crosstalk between receptor-based signaling paths of ET and plant growth regulators/related moieties; however, detail mechanisms are not clear till date.

## 5. ABA complements ethylene mediated quiescence strategies in submerged rice

According to experimental evidence, ABA may inhibit the growth of the inter-nodal meristem and leaf sheath of submergence-sensitive rice genotypes under water by negative effects of GA<sub>20</sub> aldehyde dehydrogenase. This possibly clues the indirect involvement of ABA to suppress the growth of the rice coleoptiles under anaerobic condition [32]. In another case, submergence-induced GAox1/3 transcripts are also downregulated by the application of exogenous ABA. The application of ABA restricts the accumulation of GA in the concerned tissues and the plants fail to execute the escape strategy. In fact, submergence-induced ET is the regulator of ABA concentration and activity in deepwater and lowland rice also. Even the catabolic activity of ABA also increases under submergence by ET induction, particularly with gene *ABA-8 hydroxylase 1* up-regulation. The triggering of ET must necessarily meet with the demand for ABA sensitivity variably in deepwater, sensitive intolerant lowland and tolerant lowland genotypes. However, for the tolerant types a special gene sequence *sub1A* encoding an AP2 type ERF that otherwise negatively regulates both ET production and sensitivity [33]. *sub1A* expression restricts the accumulation of ET responsive transcripts required to outgrow the shoot elongation. At physiological level, *sub1A* outgrow the inhibition of shoot coupled with regulated carbohydrate metabolism. *ABA-8 hydroxylase 1* consequently converts ABA to 8-hydroxy ABA which in turn catabolized into phaseic acid (PA). In addition, under submergence there recorded a depleted transcript for ABA biosynthesis genes like *Os ZEP*, *Os NCED1/2/3* etc. in rice seedlings. Therefore, the tolerant genotypes not only reduce the sensitivity of ET induced gene expression by regulation of *sub1A*, but also access the functionality of ABA for facilitation of suppressed growth [34].

ABA undoubtedly is a pivotal growth regulator in almost disciplines of growth and development as well as stress response. A question by default is raised that how the

ABA could send the different stress signals from the environment even with commonness of dehydration under soil-moisture deficits and submergence. Numbers of proteins of the plant cell membrane, particularly on chloroplast are reported as putative ABA receptors; however, their precise roles are yet to be deciphered. The molecular signaling for ABA reveals almost 14 members of proteins in *Arabidopsis* which are identified to interact with ABA. These proteins classically belong to pathogen related proteins and included under type 2C protein phosphatases. On ABA counterpart these proteins upon binding to ABA induce a pyrabactin resistance like (PYL) protein to associate with type 2C protein phosphatases (PP2Cs) such as ABI1/ABI2 those inhibits the activities [35]. These proteins are collectively called PYLs. In plants, the common PP2Cs include ABI1 and ABI2 those replace the ABA signaling in downstream [36]. PYLs could inactivate PP2Cs on presence of ABA and that establishes the PYLs and assists as core of ABA. In brief or for simplicity PP2Cs including ABI1 and ABI2 are set as the principal components for ABA signaling those replace the ABA responsiveness at initial step [37]. It has also been noted that PYLs may down regulate PP2Cs to perceive ABA signaling and that indicates PYLs may act as co-receptor for ABA. The protein structure of PYLs from the START (Star-related lipid transfer) family has an ABA binding site. The binding of ABA and PYLs also increases by several fold when a phosphatase for ABI2 is present [38]. The binding site of ABA for PYLs is shared by both PYL9 and ABI2 where ABA acts as binding agent. Another intuitive explanation suggests a conformational or allosteric change of PYL9 is required to develop the binding ligand on ABI2 when ABA is present [39].

Therefore, the exact molecular mechanism of ABA recognition and ABA-mediated inhibition of PP2Cs by PYLs, the isolation of PYLs is required. The cloning is also done from cDNA library of *Arabidopsis* for PYLs and PP2Cs. The over expression of those proteins is also done which is analyzed through homogeneity and crystallization procedure. The precise structure of PYL2 in both ABA dependent [ABA (+)] and ABA independent [ABA (-)] is revealed to have a catalytic core domain of ABI1 [40]. As a whole, the regulation and signaling of ABA at molecular level may summarize: first, presence of PYLs for ABA receptor but less chances to be the co-receptor; second, ABA binding is responsible for allostereism phenomenon on PYLs that in downstream induces binding with PP2Cs and third, ABA in conjugation with PYLs could inhibit PP2Cs that may hinder the substrate protein entry.

## 6. *sub1A*: The promoters have variable elements compatible to other stressors

*sub1A* has already been established as submergence tolerant gene discovered in FR13A. Later on, few *IR64* and *IR64-AUB1* have been identified with this fac-

tor and that might partly explain the level of differences between these two under submergence. The promoter of *sub1A* with its comparative sequence analysis in two distinct alleles (*sub1A* and *sub1B*) reveals the occurrence of a few single nucleotide polymorphisms (SNPs), variable in number. Few of those may represent allele-specific regulatory sequences or cis elements those are specific for upstream targeted TFs [41]. Few of those in *sub1A* allele may constitute putative motifs. SNP4 may comprise a SITE 1 motif that is alike to G-box which was first found in a proliferating cell nuclear antigen (PCNA) promoter and cloned from rice. Site 1 element in fact is transcriptional activators which is responsible for specific meristematic tissue expression. Likewise, SNP 5 in *sub1A* alleles constitutes two distinct cis elements for CAREOSREP1 motif. In rice coleoptiles, this CAREOSREP motif renders the GA-induced responses for the proteinase gene [42]. In context to *sub1A-2* allele, there recoded three SNPs like SNP3, SNP5 and SNP9 responsible for allele-specific putative cis-regulatory elements. Of those, SNP3 covers an ABA-responsive motif (ABRE). The latter is proved with almost ABA-responsive genes in plants having a core sequence GAATCC and thereby suggesting the ABA dependence of *sub1* QTL. Submergence often induces an in-built dehydration stress in rice plants and there in contiguous to ABRE other cis elements are also found in *sub1A* as dehydration response elements or C repeats (DRE/CRT) in SNP5. These are found in many drought-responsive genes in *Arabidopsis* and rice [43]. SNP9 constitutes a site II motif which represents the response elements which is seated on more upstream in transcription start sites of *sub1A* allele. Last but not the least, a third site (site III) basically corresponds to 5'-AAACCCTAA-3' in cell proliferating nuclear antigen promoter but acts as transcriptional activator. Unlike *sub1A-2*, *sub1A-1* may not have the real TELO-BOX motif but substitutes with two truncated motifs with displayed sequences: 5'-ACCCTA-3' and 5'-AAACTT-3'.

*sub1A* has been well-recognized in its concurrent occurrence with other differentially expressed genes (DEG) allied to confer submergence tolerance. This was mostly detected in *IR64* and *IR64 sub1A* at their intermodal tissues duly quantified by q PCR platforms for expression profiling of genes transcription factors. A total of 2508, of which 2487 were novel transcription factors were derived from annotation with existing databases [44]. This analysis predicts around a sequence of 2 kb stretch as upstream of almost the Deutsche Forschungsgemeinschaft (DFGs) promoter with 32 motifs. According to the activation by different allied sub-stressors (anoxia/ hypoxia, carbohydrate metabolism, irradiance, ABA, GA and other hormonal elicitors etc.) these are divided into four groups. Similarly, under submergence, the unavailability of irradiance and hypoxia appears to involve the responsive motifs in their cis-elements as ANERO1-4 and GT1CONC4:C36SENSUS, respectively in almost the DFGs [45]. For the anaero-

bic energy metabolism, there are about 16 recognized motifs, common of those PYRIMIDINEBOXOSRAMY1A, TATCCAOSAMY etc. For the carbohydrate metabolism with amylase promoter RMY motifs is the most important in both up and downregulated DFG in *IR64*, *IR64 sub1A*. For the amylase gene AMY-3 motif with the core sequence (CGACGO), essentially GC loaded was found to act as a coupling element in the association of G-box elements. In rice, MYB protein is an interconnector of hormone-sugar metabolism and distinct AMY motifs are also found, the most conserve sequence is TATCCA offering the cis-elements for TFs of *OsMYBS1*, *OsMYBS2* and *OsMYBS* [46]. For the GA metabolism, the response element as GARE and RAMY1A is important for their involvement in the inhibition of solubilization of carbohydrate in culm and leaf sheath. In rice grain protein, gluten also is characterized with gene *OsGluB-1* having four GLUB1 motifs with exclusively endosperm bound expression. In recent literature, gluten has been identified as another foremost energy-yielding protein in rice grains subjected to induce dormancy. There are also some motifs amenable for TFs like TATA box, EF1, EF2, expression of meristem genes like LEAY-TAG and also with some genes in homeotic development. In respect to IR 64, 80% upregulated genes contain EF2 motifs but few in downregulated genes [47]. Dehydration/Cold response elements as DRE/CRE and ABA response elements (ABRE) are contiguous with four of the DFG motifs more frequent. Though submergence often induces some sort of nutrient deficiency like Fe, still motifs for those like IRO2 are less recurrent [48]. At the molecular level also that submergence is integrally coupled with dehydration and ABA mediation response to recovery has been advocated with the frequency of DRE/CRT and ABRE motifs present in almost DFGs.

## 7. Physiological attribution of ethylene in rice to endure submergence stress

Two basics are applied to consider ET as a key to forward rice plants in way of submergence: submergence escape/avoidance and submergence quiescence. In conferring to quiescence, ET must be regulated by *sub1A* ERFs in different motifs along with other differentially expressed genes that could tender a feedback inhibition of ethylene. Plants under deepwater situation can withstand the flood so long that elevating water regime outruns plant standing. Occasionally this ensures the waterlogging sensitivity of the plants, particularly effective to tall *indica* genotypes. Still, submergence tolerant lowland genotypes were also exposed to inundation but did not continue beyond two weeks. Tolerant genotypes are well competent to acclimatize within these days by their subdued growth and regulated anaerobic mode of respiration. For the escape strategy, there are fair accumulation of ET and its command on GA over-synthesis resulting in increased plant height. Whatever the case is, the adaptation under flooding be-

tween two types of strategies may be due to gene duplication of *sub1* locus with distinct recurring submergence regimes. Submergence not alone exerts its ill effects but also with other multiple factors like timid diffusion of gases, improper membrane activity, fall in root hydraulic conductivity, inefficient light transmission, variable temperature, low nutrient acquisition etc. [49] (Fig. 2). In rice, submergence tolerance is mediated by a cluster of putatively expressed genes: *sub1A*, *sub1B* and *sub1C*. *sub1B* and *sub1C* cover for all rice genotypes invariably in all accessions but *sub1A* is exclusively present in submergence tolerance-specific rice genotypes [50]. *sub1A* in fact is an allele that encodes an ERF. The molecular mechanism of *sub1A* mediated tolerance has been attributed in quiescence strategy by specific gene cascade (Fig. 3). Likewise, in escape strategy rice plants are expressed with SNORKEL1 (SK1) and SNORKEL2 (SK2) through ET mediated GA accumulation in stem and leaf sheath under deep water condition [51]. Contrarily, in quiescence SLENDER RICE 1 (SLR1) and SLENDER RICE LIKE1 (SLRL1) are involved with ABA mediated down-regulation of GA influence on carbohydrate metabolism. The latter otherwise controls the mobilization of carbohydrate to the developing tissues under water and restricts the growth of plants under water. Now, submergence also reinforces the status of water deficits; however, partially in tissues even under water in excess. Physiologically, rice plants are trailed with inadequate hydraulic conductivity on roots membrane due to insufficient rhizospheric dissolved O<sub>2</sub> under submergence. Considering the energy dependent water uptake through aquaporins like channel proteins, rice roots are depleted with ATP under anaerobic energy paths to maintain quiescence strategy [52]. This essentially ensures the founding of root moisture tension depletion even under water in excess. Moreover, at cellular level the co-linearity of water deficit or dehydration stress with submergence may be approached with ABA interference on membrane permeability to uptake water down the concentration gradient also. Additionally, genes concerning the ET signaling cascade reported to play important roles in resistance to drought stress. Likewise, in rice genes like Tomato stress-responsive factor 1 (*OsTSRF1*), an ERF based transcription factors are expressed in development of osmotic and drought tolerance [53]. Another factor like ET responsive factor 3 (*OsERF3*) modulates drought tolerance by interacting with drought responsive factors (*OsDERB1*) in negative regulation of ET sensitivity [54]. ET responsive factor 71 (*OsERF71*) is reported to be strongly promoted by drought and salinity that enhances drought tolerance specifically for root structure through cell wall loosening activities and lignin biosynthesis in rice. Collectively, these situations must set a hesitant physiological and metabolic status for energy-yielding mechanism, light energy harnessing and its chemical transformation, maintenance of source-sink continuum, cellular pH and redox stabilization. In reply to these constraints, submerged plants could develop an

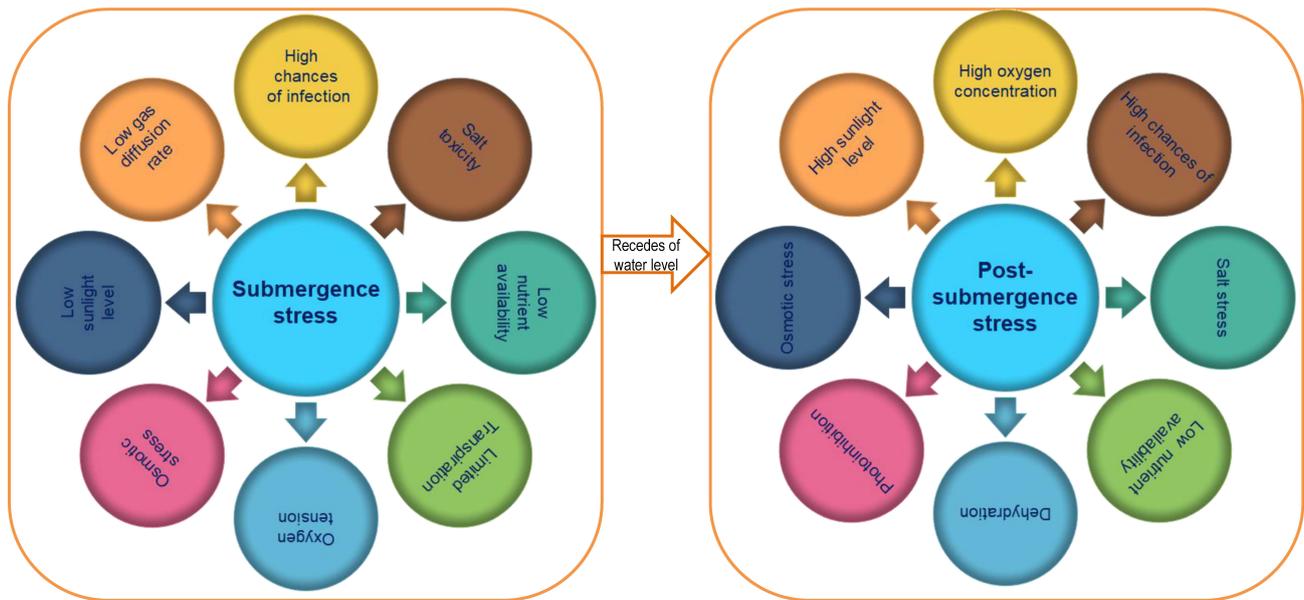


Fig. 2. Various effects of submergence and post-submergence stress in rice varieties.

altered mode of metabolic profile that must not suit terrestrial plants. Understanding the role of ET if applied exogenously to the plants under normal aerobic tension, it may not imitate the same responses as applied under anaerobic condition in rice [55]. About the signaling mechanism under submergence, not any distinct compound is produced, but normal metabolites are over expressed as a function of their roles in every ontogenic changes in the development of the plants. Still, it is the ET that actually triggers the other metabolic cascade switched on in responses to anaerobic condition of submergence. Moreover, ET mediated responses are also varied with other factors including developmental and physiological, tissue types, developmental stages and its plasticity to accept the submergence impulses. Even the doses for ET in application to induce hypocotyl growth for terrestrial species may not contest with application onto semi-aquatic plants (e.g., rice) to record reduced growth under anaerobic condition [56]. With reference to flooding ABA, ET and GA have their metabolic nexus to modulate the growth, but in order to activate the dividing tissues to perceive those stimuli. Edaphic factors like light intensities are another module for plants sustenance beneath the water level. It is well referred with *Arabidopsis* mutant to receive proportional effects upon irradiances to ET induced hypocotyl elongation. The accumulation of ACC would also ratify the possible biosynthesis under the ongoing photon flux density of ET and thereby its impact on hypocotyl elongation [57]. In rice, study supporting ET biosynthesis under light control has not been put forward. Therefore, undeniably, ET signaling and its effects on growth regulators must be more elaborately resolved to find out specific turn of quiescence mechanism exercised with *sub1* factor.

## 8. Signaling paths depend on other metabolites paraphernalia under anoxia

Genes expression under submergence-induced anoxic condition are not independent, rather those are directly or indirectly correlated with other expression webs under dehydration, metal toxicity, pH variations, light intensities differences and also biotic infestations. Still, it is the ET that may corroborate all of these signaling by connecting in a more complicated cascade which has been exercised by *sub1A* encoded group VII encoded ERF belongs to AP2 sub-group are quite compatible to other differentially expressed genes under anoxia as well as oxidative redox. Even terrestrial species has been reported with five ERF-VII gene(s) expression under anoxia and ROS induction and have been cloned from *Arabidopsis* [58]. It is well admitted that submergence creates an oxidative stress condition that itself happens to be a stressful factor. ET plays a major/key role through ABA and GA metabolic web; however, indirectly to influence plants' survival [59]. The tissue specific accumulation of ET under submergence creates the cellular mechanism for cell growth and elongation for specially escape strategy in few deep water rice plants. This is coordinated with a simultaneous phenomenon of programmed cell death (PCD) where ET may trigger the development of ROS. In maize and rice roots, a significant amount of ROS generation induces ET accumulation that plays a major role in aerenchymatous tissue formation, particularly in those involving emerged adventitious roots [60]. Regarding the mechanism of ROS generation, its signaling and downstream impacts on ET to promote aerenchyma formation is much contextual. Likewise,  $H_2O_2$  acts as the predominant secondary messenger for ET signaling for development of aerenchymatous tissues under anaerobic stress.

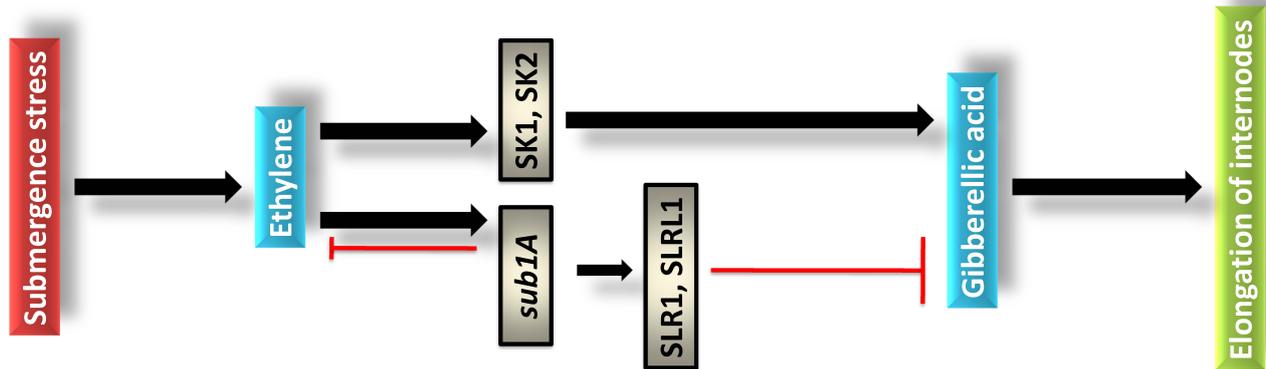


Fig. 3. Physiological and molecular function of ethylene and *sub1A* in rice plants under submergence stress.

$H_2O_2$  is not a typical free radical but are safer ROS that within the cellular threshold condition could induce many reactions favorable for plant growth. Other ROS include  $O_2^{\cdot-}$ ,  $OH^{\cdot-}$ ,  $^1O_2$  those all are the byproduct of complicated  $O_2$  metabolism under aerobic condition [61]. The latter is more experienced, particularly in rice roots when exposed to aerobic or desubmergence from anaerobic submerged condition [62]. The pathways for  $H_2O_2$  mediated hypoxia signaling at cellular level is regulated by a special enzymatic function where respiratory burst oxidase homologue D (RbohD) is responsible. This is the key regulator on initial stage of anoxia signaling that could modulate the expression of downstream anoxia-inducible genes. The identification of RbohD/EIN2-double mutant is responsible for delayed seed germination under submergence [63]. Under submergence RbohD/EIN2-5 mutation can down regulate the root growth as a well-marked phenomenon for quiescence strategy. Moreover, the vegetative character like pigment content and leaf survival are reduced in that mutant when compared with wild type under anoxic condition [64]. The expression of RbohD that catalyses  $O_2^{\cdot-}$  generation in apoplast is a biomarker for anoxia tolerance. In *Arabidopsis*, RbohD are clones of multi-gene family composed of ten Rboh genes [65]. The molecular mechanism with that RbohD displays a differential expression through developmental process that responses submergence like other abiotic stresses. A calcium dependent signaling for AtRbohD is activated under submergence to switch on cell division and adventitious roots formation [66]. In relation to  $H_2O_2$  signaling the ROS is reduced in both EIN2-5 and RbohD mutant under anoxia; however, they are induced under hypoxia and also similarly down-regulated in those mutants under same condition. Therefore, AtRbohD happens to be the key player in initial  $O_2$  depletion to plants which is linked in downstream for various responses. The relationship between ET accumulation and RbohD expression is less understood. The double mutant for RbohD/EIN5 against the wild type plant under hypoxia a lot of information has been emerged from ROS regulation. AP2/ERF like

transcription factor is also involved in signaling where ET takes the control to regulate the hypoxic stress. Thus, the secondary messenger,  $H_2O_2$  production have been implicated in  $O_2$  deprivation tolerance. Till date, the hypoxia-induced transcript level of hypoxia promoting genes those could encode ET responsive factors 73 (ER73) is down regulated in those mutants [67]. This probably suggests the possible existence of others ROS signaling elements besides ET and RbohD. The expression of both RbohD and EIN2 has the synergistic effects under submergence regulated seedling germination and root growth. Collectively, a synergistic consortium between ET in  $H_2O_2$  signaling is responsible in plants developmental stages in respective to  $O_2$  deprivation.

In rice, this ERFs-VII are known from FR-13 A, a semi-tall *indica* genotype as the governing elements to prolonged inundation and has sequence homogeneity with *HRE1*, *HRE2*, *RAP2.2*, *RAP2.3*, and *RAP2.12* induced under low oxygen partial pressure. In relation to submergence other tandem repeats of ERF (not *sub1*) could sense the flood in some deepwater genotypes commonly termed as *SNORKE-1* that induces culm elongation, however, directly or indirectly with GA coordination. *sub1* has got its unique sensitivity to low oxygen tension even with its post-translational modification through a sequential process. A cysteine oxidase mediated proteolysis of N-terminal end of ERF encoded protein may be involved in this alteration. This is more established with findings of various polymorphisms in cysteine oxidase, however, in *Arabidopsis* that may draw a parallel relationship in sensitivity to ET mediation [68]. So, to let ET to reduce activity the proteolysis ERF coded protein must be checked by depleted oxygen tension under submergence. Undeniably, ET is the unique growth regulator which controls its own concentration within the tissues by auto-inhibition and this phenomenon is quite causative in signaling of submergence tolerance. This cascade of signaling is involved with different transcription factors and their activation which find its binding site in many ethylene-responsive elements (ERE). Out

of those AP2/ERF, a super family happens to be the largest one in crop species and interaction with ERF in different regulation is the key to submergence tolerance in rice [69]. In most of the cases dicot species added more information in modalities of bindings with ERF and thereby the elucidation of the role of ET in diverse conditions of stressful environment is possible.

With reference to rice, the activity of ACS has been well characterized for its regulation and imposition of submergence recovery of quiescence strategies. ACS belongs to the E.C. family depending on pyridoxal phosphate (PLP) with a co-factor vitamin B5 (Pyridoxal pyrophosphate). On the amino acid residues in C-terminus there cloned three possible forms of ACS from rice and all of those perform multiple functions of carboxylation, deamination and transamination of amino acids. In rice, a number of genes have also been reported to complement responses of ACSs in meeting with a wider array of abiotic stresses. Under submergence, particularly, with anoxia activation of ACSs are mostly offered by auto-phosphorylation at different amino acid residues at their C-terminal end [70]. This is more illustrated in ACS II with a conserved serine residue that undergoes phosphorylated by calcium dependent protein kinase along with other same residues but phosphorylated with mitogen-activated protein kinase (MPK). In contrast, ACS III has no phosphorylation domain and thereby appears to be the least contributory. It has already been reported that ET has been self-regulated within its cellular concentration by the feedback inhibition of its intermediate or even byproducts also. In fact, when methionine, the precursor of ET is trailed by its concentration the former has to be recycled to maintain a steady homeostasis or to prevent end product inhibition. Methyl thioadenosine (MTA), a byproduct of ET can be hydrolyzed to methyl thioribose (MTR). The latter is again phosphorylated by a kinase into phosphorylated MTR. In downstream complex reactions with few other intermediates as well as different cofactors like Ni and Fe, the successive enzyme activities may forward a crucial regulation for ethylene biosynthesis. Other rate-limiting genes for ET biosynthesis pathway commonly concern S-adenosyl methionine decarboxylase (SAMDC) with its different isoforms: *Os SAM-DC 1/2/3/4/5*, *Os MT-kinase* etc. [71].

## 9. Anoxia compromises with energy turnover and executed in adoption by rice

Anaerobic stress in the form of anoxia or hypoxia undoubtedly creates a non-sustainable situation where plants modify their metabolic pathways, particularly with carbohydrate metabolism [72]. Considering rice as a model crop under submergence for anoxia there have been two specific growth forms those compromise with energy yielding metabolism. An illustration with rice in both escape and quiescence strategies are well familiar in this con-

cern where glycolytic flux is turned out in an anaerobic mode of metabolism, particularly with alcoholic fermentation [73]. For the escape strategy where rice plants execute more metabolic energy for growth of vegetative tissues like internodes and leaf sheaths in one way represent the constraints of lodging sensitivity. To overcome the prolonged period of submerged condition, escape strategy offers the internodal stem elongation, changes in plant architecture and metabolism. This uncontrolled growth of tissues of the concerned vegetative parts adds the plants in long height over the water regime and that causes maximum lodging sensitivity when the water subsides. Though escape strategy is a primarily adopted mechanism for flooding resistance still, from agronomic purposes it is not full proof for plant growth and yield potential [74]. From the corner of dry matter allocation, the tall indica cultivars are more partitioned with vegetative growth than to mobilize photosynthates in reproductive parts like developing grains [75]. However, this strategy would be granted as one of the pathways in avoidance for short time submergence stress. Genetic variability in existing rice genotypes thus, are based on pre and post submergence period dry matter accumulation in calm and leaf sheath to offer better insurance for escape strategy. Moreover, from allocation of photosynthetic reduced carbon plants are more prone to convert those into starch rather than sucrose in those vegetative parts [76]. So, plants have to execute more energy in turnover of starch-sucrose interconversion to make readily access for transportable sugar (sucrose) and its utilization into glycolytic pathways. Escape strategy is also set back for oxidative exposure and waterlogging, particularly under intense illumination of natural sunshine. The changes in photosynthetic pigment more into light energy harnessing (PSII:PSI, chlorophyll a:b and chlorophyll:RuBisCO) than energy quenching mechanism lead the plants to photo oxidation. Rice being a C<sub>3</sub> plant is thus not filled with possible drawback of over growth in vegetative tissues as found in escape strategy against flooding [77]. This is equally attributed with cellular level metabolomes those principally covers fatty acid degradation, promotion of carbohydrate transport, turnover of sucrose to starch interconversion, auxin mediated root emergences etc. [78].

Anaerobic germination is the key feature in submergence during seed germination and set of seedlings condition. In low land ecosystem, the few rice cultivars are led to direct seeding practices by the farmer where anaerobic germination evaluates the potential of germplasm under submerged anoxic or hypoxic soil in low germination rate ensuring seedling death. Still, rice germplasms with their ability to grow on that hypoxia to anoxia following complete submergence during vegetative growth, particularly at seedling stage for a prolonged period offer another strategy before the flood recedes [79]. The existing rice germplasms with particular reference to FR13A like land race possessing a gene/QTL offers the quiescence strategy for submer-

gence tolerance at vegetative growth [80]. The quiescence strategy technically refers the economization of carbohydrate metabolism in calms and leaf sheaths that checks the overall plant growth under water. The conservation of carbohydrate in the vegetative tissues and its less utilization in major glycolytic path leads the suppression of plant growth; however, for a particular period of submergence [81]. This essentially turns out major glycolytic path into alternative mode like anaerobic catabolism and that is commonly referred with alcohol fermentation. Therefore, quiescence strategy is principally based on utilization of carbohydrate metabolism into fermentative catabolism of sugars with less production of energy equivalent (ATP). Physiologically this strategy is facilitated with one of the major plant growth substance ET and its domination over others growth hormone like GA, auxin, ABA etc. So, ET-dominated growth substitution is the principal characteristic feature for quiescence strategy where plants could able to sustain their life under water mostly by suppression of growth that requires less energy. Therefore, plants under such flash flood condition reduce the exhaustion of carbohydrate/nutrient within few days and thereby, plant growth is prohibited that may reveal after occurrence of flooding situation. Therefore, with less cellular energy utilization and shortage of carbohydrate in downstream growth period, the plants may hinder to growth and development [82]. With quiescence strategy plants are strengthened with respiration just for shake of viability of tissues under constrain of anoxia and hypoxia rather than growth respiration which ensure the overall realization of adequate growth [83]. Plants are characterized with delayed flowering, down regulation of cell wall loosening, down regulation of ET production etc. in quiescence phenomenon. Moreover, the plants' differential responses to insufficient O<sub>2</sub> tension (under submerged tissues) limit the respiratory pathways those are detrimental to plant sustainability.

## 10. Signaling paths of ethylene perception are diverse with different factors

In rice stimulus-response mechanism under submergence particularly, with ET often is dependent on a prokaryotic two-component system of a bacterial histidine kinase [84]. This is accompanied by another histidine-containing phosphor transfers enzyme pertaining to the signaling across the cellular membrane. Rice, plants are aided with other secondary messengers in forwarding the stimulus, particularly, the anoxia and elevated redox at post submergence stress. The proteins of those systems correspond to ethylene insensitive homologues: EIN2, 5, 1. Those are also accompanied by others like orthologues of constitutive triple response (CTR1). In rice several receptor proteins have been cloned with overexpression imparting sensitivity to ET under submergence includes *OsERS1*, *OsERS2* [85]. The other sub-families are common with their

variable responses and important of those are *OsERT1*, *OsERT2* and *OsETR3*. The other common responses of ET includes triple responses which is also facilitated in signaling pathways for any kind of stress impulses. *CTR1* is the most important of such those expressed proteins which is dominant in absence of ET. *CTR1* is a recessive mutation which may be active in constitutive activation of ET functioning. In case of wild type, the gene produces a negative regulator for responses done by the paths ET, whereas its mutation can activate the responses of the ET. *CTR1* is an analogue of the Raf family gene whose characteristics include a serine/threonine protein kinase [86]. In a number of cases starting from yeast to higher angiosperm the kinase is involved in many developmental as well as signal transduction pathways. In response to submergence tolerance encountered by ET the order of action with *ETR1*, *EIN2*, *EN3* and *CTR1* has been ascertained by the expression of epistatic relationships of mutants. In rice there recorded three distinct *CTR1* genes have been cloned: *OsCTR1-1* and *OsCTR1-2* have the closer proximity to *CTR*. For other genes like *EIN2* rice acquires many polymorphisms that commonly represent *OsEIN2/MHZ7*, *OsEIN2.2*, *OsEIN2.3* and *OsEIN2.4* homologs. *CTR1* is a protein kinase that phosphorylates *EIN2* at a specific domain in absence of ET. In absence of ET the *EIN2* is activated and forward the downstream signaling of triple responses. On such activation, the hydrolyzed part of *EIN2* is transduced into the nucleus and activates the other downstream moieties like *EIN3*. In rice other *EIN*-like residue has also been reported and appears to be the key regulators in binding to ERE sequences [87]. Therefore, *EIN3* is proved to be a novel transcription factor that finally regulates the signaling of ET function. In *Arabidopsis* ET signaling pathways is predicted to be the model taking *ETR1* as a primary receptor. *ETR1* in presence of ethylene suppress the negative regulator *CTR1*. On such condition, other signaling protein *EIN2*, which opens the ion channel on the membrane, can lead to the transducer of the signal into the nucleus. Thereby gene activation is achieved. This is the model pathways that are also appreciated in rice with significant variations in different mutants. Likewise, *OsERF1* is another member of the ethylene responsive sub-family which is expressed in rice with a significant variation to ethylene sensitivity. The sensitivity is also adhered to the other stressors inducing an anoxic or hypoxic condition of plants.

Now, submergence is also related to a number of facets where the abundance of water brings upon high salts and tilts, temperature variation, fluctuation of pH, excess heavy and toxic ions as well as other toxic substances. Despite other plant growth regulators, it is ET that takes command overall of the physiological processes under submergence to be modulated. On the gross level of phenology, ET plays major role in the development of roots and shoots, which is adventitious in nature, along with intermodal growth, formation of the abscission zones, develop-

ment of air vacuoles etc. [88]. Therefore, the signaling essentially covers an extended network from nuclear origin to physiological responses through metabolic cascade. Likewise, water in abundance, or the hypoxic condition, would be another target of photosynthetic research in cereal, the major impeded crop under submergence. Starting from gas exchange through stomata ending to carboxylation in mesophyll tissues would be more interesting for the rice genotypic plasticity to adopt the stringencies of the anaerobic condition of submergence. Attenuation of chlorophyll fluorescence with its non-photochemical quenching of the dispersed solar intensity under water would clarify energy dissipation paths and alteration of the targeted leaf tissues. Following photosynthetic events, it is the allocation of sugars that faces more vulnerability to submergence induced anoxia. Signaling to this case is initiated from starch mobilization for glycolytic operation in rice coleoptiles under complete to partial submergence. With reference to rice, O<sub>2</sub> deficiency could set the expression of  $\alpha$ -amylase in the seed coat pressed tissues of aleurone layer. Rice has developed with distinct variations of  $\alpha$ -amylase polymorphisms (AMY1AC, AMY2A, and AMY3A-F) more sensitive to anaerobic condition. This is more illustrated in the case of elongation strategy where a rapid depletion of sugar level corresponds to the expression of GA [89]. In some quiescent exercise genotypes like FR-13A, the insensitivity of GA is due to the absence of upstream elements sugar response core. This also corresponds to the transacting factor appreciated by those elements in the association of few coupling elements. Such of those is represented by another class of non-fermentative receptor kinase 1A (OsSnRK1). Moreover, another calcium-dependent protein kinase B, CIPK15 is reported to have an impact on sugar-depleted signaling, specifically for the genotypes exercising quiescence strategy [90]. Translocation of reserve photo assimilates would be more interesting to mark another module of signaling under submergence. Both assimilation of sucrose and its allocation into others carbohydrates are regulated by the O<sub>2</sub> deficit environment in rice fallows with distinct moderation of gene expression. In fact, sensing the sugars depletion under such a condition and thereby moderate the downstream sugar metabolism would be a critical point to adopt tolerance in seed germination following early withstanding of plants.

## 11. Adoptive strategies in sugar and nitrogen metabolism under anoxia

To maintain an altered glycolytic path and reduction of ATP consumption, there are the two basic domains on which submerged plants could adopt depleted redox of submergence. There are two key genes in the starch mobilization of shifted glycolytic paths into anaerobic mode of metabolism. Initially a sucrose phosphate synthase (SPS) is reversibly activated with uridine diphosphate (UDP) as

a glucose carrier [91]. The second one is sucrase or invertase in -non-reversible reaction hydrolyzing into glucose, however, in phosphorylated form. In fact, at the cellular level these two gene products are opposing in function to sustain the consumption of ATP in a more economical way. In presence of UTPG and fructose the enzyme SPS can act with one mole of PPI residue. In another round of reaction, UTP is used for fructose phosphate with the synchronized generation of ATP. The enzyme is nucleotide diphosphate kinase. Conversely, invertase requires extra ATPs in the hydrolysis of sucrose than SPS mediated reaction. Under the condition of O<sub>2</sub> deficit like submergence, therefore, the key regulator is expected to be the SPS in terms of ATP concentration sustenance [92]. Even at the gene regulation level also the submergence along with starch depletion would be more favorable for more expression of SPS than invertase. Therefore, sugar sensing would be more lenient to SPS expression both of its economic provision of ATPs as well as establishing the starter of the glycolytic cascade through the fermentative mechanism. In rice, particularly, for those of quiescent exerciser other variants of PFK (*Os PFK*) and hexokinase (*Os HXK*) are also overexpressed under anoxia or submergence. These genes are also in the coordination of other fermentative mechanisms employing ADH activity under the O<sub>2</sub> deficit condition of submergence, particularly, in rice seed coleoptiles [93].

The calamity for sugar metabolism management under anoxia is predominantly managed by lactate and pyruvate reactions, however, in anaplerotic paths. Two genes in order of regulation like PDC and lactate dehydrogenase are the keys to carry forward plants switching over aerobic to anaerobic mode of metabolism. Still, the energetic plants are trailed for ATP generation in a more economic mode. In the oxidation of NADP(H) + H<sup>+</sup>, the glycolytic mode of respiration takes away plants' pivotal energy-yielding metabolism in an altered manner that sets the discrimination between escape and quiescence strategies. Still, for the quiescence strategy, ethanol formation may trail the lactate in rice where significant toxicity is referred with the latter; rather ethanol is more supplementary to partial O<sub>2</sub> pressure [94]. A complicated feedback regulation has been the feature of plants where a remarkable shifting of pyruvate metabolism via TCA intermediates is attributed to the changed affinity of the enzyme to substrate. This semblance to the fate of pyruvate under low tension of O<sub>2</sub> as that of submergence, particularly, for the quiescence-loving genotypes. There recorded a significant reciprocal regulation for pyruvate dehydrogenase (PDH) activity to the PDH kinase to dominate the pyruvate metabolism under anoxia. Still, PDH regardless of plants from any ecological niche could better survive through its overexpression under depleted oxygen. In rice, two major isoforms: *PDC1* and *PDC2* are reported to be overexpressed both of its transcripts and proteins [95]. Tissue specificity is featured for both of those isoforms to be over-expressed in rice that also

is a possible clue for elongation and quiescence strategies. In fact, a shoot is more compatible to response the anoxia by elongation with over expressed *PDC1* than roots. Under complete submergence, particularly for those of quiescence exerciser, sustenance is more preferred to the roots where *PDC1* is less contributed [96]. It has more been illustrated with a report for a diurnal change in the activity of *PDC1* and *PDC2*, more in roots at night than a day where plants meet a solemn condition of oxygen deficiency. This would predict the survival of rice; even in other aquatic genotypes is based on fermentation reactions in shoots to support anoxia for the more growing photosynthetic tissues than roots. Still, the sensitivity of the root to fermentation metabolism is alike among the genotypes under the same condition of O<sub>2</sub> depletion. In contrast to PDC, ADH, with its isoforms (*ADH1* and *ADH2*) may not be appeared as a major determinant to support the alcoholic fermentation to sustain under submergence [97]. Besides, ADH would be another supplementary access to substitute carbon source attainable for post-submergence stress, when tissues become re-oxygenated on air. Still for coleoptile growth and its downstream activities ADH would set a physiological marker to select rice genotypes for initial tolerance to waterlogging. Therefore, regarding the energy conservation under submergence rice plants have the unique ability restore ATP in an alternative mode displacing the normal glycolytic reactions. As alternative sources of energy, proteins, fats would be other choices through gluconeogenesis paths to support the energy mediated survival of plants under oxygen deficiency. Fermentation would be the most effective measure to endow with more ATPs even for both the quiescence and escape strategies. However, for the latter it is to afford more energy to support the elongation ability of the internode and leaf sheath [98]. GA metabolism happens to be targeted through its over-expression detouring the ABA paths, still, not impeding the all-purpose of growth. Under depleted oxygen tension, plants could recover the oxidized form of NADP<sup>+</sup> by the sluggish rate of electron flow but sustain the cellular redox. Out of a number of determinants the depleted oxygen could be overcome by the maintenance of cellular pH with inorganic phosphate (Pi) in parallel to normal ATPs supplementation as in glycolysis.

## 12. Conclusions

Scientific perceptive and its analysis to submergence mediated hypoxic or anoxic stress in wetland species is appeared to be the most complicated with different facets of cellular, metabolic reactions. From the most pioneer approaches, it covers predominantly fermentative metabolism *vis-a-vis* a shifting of normal glycolytic paths extending the gene-web governed cellular signaling. This is more impulsive with other facets of the responses when plants are transferred from complete anaerobic condition (submergence) to the high O<sub>2</sub> tension phase (as

post-submergence/de-submergence period). Collectively, all these episodes frequently meet with other elements of plant's cellular responses like ion homeostasis, redox potentials, pathogen sensitivity, tissues specific signaling, sugar sensing, protein-protein or DNA-protein interaction, high throughput regulation of mi-RNA etc. With more advent of technologies through proteomics studies the changes of specific proteins during or after submergence period might be identified as candidate gene to select the appropriate rice genotype for flood tolerance. With reference to rice, *sub1A* QTL with exercise of quiescence strategy is the choice for breeders to dissect and characterize for better understanding, (still, not all for seedling survival) to design crop architecture/designing between and within genotypes under such oxygen-depleted soil. Admitted well the knowledge gap for seedling germination even under anoxic condition *sub1A*-mediated triggering of not being the sole factor, the importance of flood tolerance is still dependent on quiescence paths. Likewise, the collective interaction of AP2/ERFs gene(s) families and their impact on ethylene performances would be physiological modules to select the tolerant genotypes under such anoxic condition. In another approach differentially expressed transcription factors in *sub1* bearing genotypes and their association in other cellular modules of dehydration, oxidative stress would be relevant to identify the tolerant genotypes. Both structural and functional proteomics in relation to protein quantification, peptide identification and validation, protein assignment and finally protein list would be made from mass spectrum data. The all complicated but effective proteomics approaches would define the functional genomics in deciphering the expression pattern under particular condition. Between and among the varieties the differential proteomics would be another approach to study the variation of rice genotypes under identical or varied condition of submergence.

## 13. Author contributions

MKA and MH conceived the idea and made the outline of the manuscript. MKA, IS and DD collected the literature and wrote the manuscript draft. MH edited the manuscript and prepared the figures.

## 14. Ethics approval and consent to participate

Not applicable.

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## 17. Conflict of interest

The authors declare no conflict of interest.

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