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Breeding for flooding tolerance in rice: Advancements and future perspectives

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Abstract

Rice, the resilient grain, is cultivated in different types of ecosystems, from seacoast to hilly areas. Unfortunately, due to climate change, it frequently suffers from submergence stress during its growth period. Anoxic stress at the germination phase, flash flooding during the vegetative phase and water stagnation in low-lying areas are the major types of flooding in rice. When floodwaters rise, rice adapts. Some varieties stretch their stems toward the surface, gasping for air. Others remain dormant, conserving energy, like the FR13A landrace, *SUB1* equips rice with underwater endurance. It orchestrates a genetic symphony, fine-tuning metabolic pathways and signalling survival. Some of the promising quantitative trait loci (QTLs) identified are qAG-9-2, which is responsible for anaerobic germination tolerance; qSUB1 for vegetative stage submergence tolerance, and qTIL12 for deep water adaptation. Identifying other novel QTLs and donors helps to breed varieties tolerant to different types of submergence stress. Along with Swarna *SUB1,* many mega-submergence-tolerant varieties have been developed and released for cultivation in Asia. As we cultivate these versatile survivors, we sow hope for a food-secure future.

Keywords

Rice; submergence; anoxic stress; flash flood; qSUB1

Introduction

Rice (*Oryza sativa*) is a global staple food and is one of the three leading food crops in the world, along with wheat and maize. It is also the primary crop of India, which is widely cultivated across diverse environmental conditions, spanning from coastal regions to high-altitude areas. India boasts an extensive rice cultivation area of 47.83 million hectares, with an impressive annual production of approximately 135.75 million tonnes (1). India, being a vast and densely populated nation, faces significant challenges due to fluctuating weather patterns. The repercussions of natural disasters like floods and droughts pose substantial threats to crop production. Among the abiotic stresses' the vast majority of deltaic and coastal plains of India are prone to flooding during germination, seedling, or vegetative stages of crop growth. According to official statistics, around 15% of India's total land area, that is, 49.82 million hectares, is highly vulnerable to floods (2). It estimates that approximately 12–14 million hectares of India's rice-growing area is prone to flash floods. However, it is worth mentioning that in these

areas affected by floods, rice productivity stands at a low average of 0.5–0.8 tons per hectare, which is very low when compared with favourable lowlands where rice yields can go up to 2 metric tons per hectare (3). Another data indicates that India experienced 304 major flood events between 1950 and 2020. These catastrophic floods had a profound impact, affecting approximately 895 million people and costing USD 84 billion (4). Given the escalating global temperatures, uncontrolled urban expansion, and environmental deterioration, it is probable that both the frequency and severity of flood risks in India will heighten (5). In view of the above-mentioned problems, this review deals with the rice-growing agroecosystems in India, types of flooding stress, different types of stage-specific mechanisms adopted by tolerant genotypes and available donors, QTLs identified, and their utilization in breeding programmes aiming to develop submergence-tolerant rice varieties and future perspectives.

Rice growing agroecosystems in India

Rice is grown in different ecosystems and agroclimatic regions. India's rice-growing agroecosystem can be broadly divided into five types: I) Rainfed upland: direct-seeded rice is cultivated as a rainfed crop in upland areas of Assam, Bihar, Odisha, parts of Madhya Pradesh, the eastern part of Uttar Pradesh, the northern hills of West Bengal, and the north-eastern states. II) Rainfed lowland: It is typically transplanted in fields. These fields are carefully levelled and bunded to retain surface water. However, the depth and duration of flooding exhibit significant variation during its growing period. It is grown in the North-Eastern, Eastern, and Western regions of India, which constitute a total of 14.4 million hectares which accounts for 32% of the total rice cultivation area. III) Flood recession irrigated: It is mainly cultivated in flood-prone areas of the Brahmaputra river in Assam, and Ganga and Mahanadi in the eastern zone of India, which comprises Orissa, Jharkhand, UP, eastern part of Bihar, Chhattisgarh, MP and west Bengal. IV) Irrigated: Nearly 50% of the country's total rice crop area is covered under irrigated rice fields in India which are mainly cultivated in bunded fields and deltaic regions of the Mahanadi, Godavari, Krishna, and Cauvery rivers of the Southern region and in the Indo-Gangetic plains of Punjab, Haryana and Uttar Pradesh. V) Deep-water/floating: It is grown in the floodplains and deltas of the Ganges, Brahmaputra, and coastal areas. Deep-water rice is commonly grown in standing water with a depth of 50 cm to 400 cm or more, or in daily tidal changes that occasionally even result in total submersion. Deep-water rice occupies 11.4% of the total rice area in India (6-9).

Types of flooding stress

Rice production in India is often severely affected by various biotic and abiotic stresses at different growing stages (10). Indian agriculture is always a gambling of monsoon rains; erratic monsoons have frequently caused floods leading to submergence or water-logging conditions (11). Flooding stress in rice is of three types, *viz*., anoxic stress at the germination phase, flash flooding during the vegetative phase, and water stagnation in low-lying areas.

Direct-seeded rice (DSR) is becoming increasingly popular in India due to its cost efficiency and convenience (12). However, due to heavy rainfall, flooding could occur immediately after seeding, which leads to hypoxia (low oxygen) or anoxia (complete absence of oxygen), leading to anaerobic germination (AG), seedling death, and poor crop establishment. AG is the first type of flooding stress, which is the primary challenge to the widespread adoption of DSR (13). The second type of flooding stress is mostly caused by the regular flooding that happens in rain-fed lowland parts of India during the monsoon season when cultivating rice. This flooding causes the rice crop to completely submerge for ten to fifteen days during the vegetative development period (flash flooding) (14). Cultivation of rice in low-lying and near swampy areas of backwater or near river basins leads to stagnation of water (up to 50cm) for a prolonged time, leading to a third type of flooding stress called extended water stagnation stress (15). The fourth type of stress is called deep water stress, which is mainly due to the continuous raising of water (50 cm to 400 cm) in rice fields of flood plains, deltas and coastal areas (16).

Flood tolerance mechanism in rice

Rice plants have the evolutionary ability to tolerate partial submergence and waterlogging due to the presence of an aerenchyma system that enables aeration. Rice is the only cereal crop which can be grown in an ecosystem that is flooded (17). Certain rice varieties have good anaerobic water germination capabilities (18). Other tolerant rice genotypes adopt different strategies, like remaining dormant underwater until the water recedes (quiescence strategy) or elongating the stem, thus escaping the stress (escape strategy) (19).

Rice under submergence mainly deploys three types of stage-specific adaptive mechanisms. 1) Anaerobic germination tolerance mechanism. 2) Quiescent strategy during seedling stage and 3) Escape strategy in deep-water rice.

Anaerobic germination tolerance mechanism

In rice, seed germination and seedling growth are mediated by a series of physiological and biochemical events. Rice seeds, upon imbibition of water, trigger the synthesis of gibberellic acid (GA) in the embryo which diffuses to aleurone cells and activates the production and release of α-amylases in the scutellum, where the breakdown of nutrients and starch begins (20-21). Upon hydrolysis, these sugars, reduced nitrogen, and other soluble nutrients are adsorbed by the scutellum and transported to the embryonic axis to support seedling growth (22). However, during anaerobic conditions, the regular supply of energy is restricted, unlike in tolerant genotypes, α-amylase is expressed by GA, and the sugar starvation signalling pathway gets activated. The sugar response complex (SRC) activates the α-amylase promoter under sugar deprivation, while the gibberellin response complex (GARC) activates it upon GA accumulation (23-24). During the GA signalling pathway, the DELLA domain repressor (SLR1 in rice) is bound by the GA-GID1 complex after GA binds to

the receptor GID1. The production of GA-inducible genes is subsequently made possible by the GA-GID1-SLR1 complex binding to an F-box protein called SCFGID2 ubiquitin ligase, which targets SLR1 for destruction by the 26S proteasome (25-26). In contrast, during the sugar starvation signalling cascade, a calcineurone B-like protein-interacting protein kinase (CIPK15) causes the global energy sensor sucrose non-fermenting-1-related protein kinase 1 (SnRK1A) to accumulate. This, in turn, promotes the MYBS1-TA box interaction (Myeloblastosis Sugar Response Complex 1) and activates α-amylase transcription (27). Lu et al. (28) found that under sugar starvation in embryos, MYBS1 attaches itself to the TA box to activate the promoters of α-amylase. In rice endosperm, the GA signal interferes with the sugar suppression of the α-amylase promoter, suggesting that there may be communication between the sugar and GA signalling pathways (29). Hong et al. (30) found that nitrogen and phosphate starvation signals activate a standardized system to control the expression of α-amylase.

Like GA and α-amylase, trehalose also plays a key role in the germination process. Trehalose is a nonreducing disaccharide that serves as a translocated carbon source and a compound that protects against stress. Trehalose-6-P synthase (TPS1) is crucial for embryo development. Overexpressing TPS in otsA affects how seedlings use sugar. Trehalose-6-P (T6P) has been shown to promote starch synthesis by redox activating ADP-Glc pyrophosphorylase (31), suggesting that T6P is involved in signa-lling the chloroplast of the cytosol's sugar level and starting the production of starch. Trehalose-6-phosphate phosphatase 7 (*OsTPP7*) is an important gene in AG-tolerant lines having qAG-9-2 in rice. During low-oxygen stress, *OsTPP7* is overexpressed, which in turn regulates T6P metabolism. *OsTPP7*-containing lines have greater trehalose levels, which suggests increased T6P turnover. Because *OsTPP7* inhibits the simultaneous rise in the sucrose availability signal, T6P, which would otherwise reduce sink strength through feedback inhibition, increases the embryo axis-coleoptile's sink strength and increases the amount of sucrose allocated to growing tissues (32). This is how the *OsTPP7* helps in the survival of tolerant lines during AG and supplies energy for coleoptile elongation under submerged conditions. Yang et al. (33) found that OsTPP1 expression was notably upregulated under hypoxia at germination and bud stages; however, further studies on *OsTPP1* are required for better understanding.

Seed vigour is one of the important traits in direct-seeded rice cultivation, which plays a pivotal role in quick germination and rapid establishment of roots and shoots (12). *OsIPMS1* catalyzes leucine biosynthesis, aids in the production of free amino acids, GA, and enhances the tricarboxylic acid cycle along with glycolytic processes. It also supplies nourishment for seed germination and seedling growth, all of which have an impact on early seed vigour in rice. By interacting with *OsSnRK1A*, a regulator of the sugar signalling pathway, *OsSAUR33* controls the vigor of rice seeds. *OsHIPL1*, a new gene that also controls rice seed vigor, increases the expression of endogenous genes linked to ABA synthesis (*OsZEP* and *OsNCED4*) (34-36).

Coleoptile elongation under anoxia is an important mechanism adopted by AG- tolerant lines by using cell expansion and expansins (EXP) (37). EXPA2, EXPA4, EXPA7, and EXPB12 expression patterns in coleoptiles from aerobic and anaerobic seedlings were studied and it was found that the mRNA levels of EXPA7 and EXPB12 appear to be higher under anoxia at 2 to 3 days after germination, which coincides with the anoxic coleoptile elongation phase; EXPA2 and EXPA4 were less abundant under anoxia during the first 4 days of germination. This suggests that EXPA7 and EXPB12 regulate coleoptile elongation under AG. The expression of transcription factors (TFs) linked to alpha expansin and beta expansin was shown to differ between tolerant and susceptible lines in a comparative transcriptome analysis of developing rice seedlings exposed to individual and combined anaerobic and cold stress (38-39). A large QTL controlling coleoptile length under submergence was discovered during the characterization of the gene encoding the UDP glucosyltransferase (*OsUGT75A*). It was discovered that *OsUGT75A* mediates the interactions between JASMONATE ZIMDOMAIN (OsJAZ) and ABSCISIC ACID-INSENSITIVE (OsABI) proteins, which in turn accelerates coleoptile length. This is achieved by lowering free abscisic acid (ABA) and jasmonic acid (JA) levels by encouraging glycosylation under submergence (40).

α-amylase plays a crucial part in starch degradation. Rice ALPHA AMYLASE 3 (*RAmy3D*) is one of the α-amylase-encoding genes responsible for starch breakdown in developing rice seeds. Since its promoter lacks a GA-response cis-acting region, *RAmy3D* cannot be induced by GA; nonetheless, it can be sugar-regulated. While *RAmy3D* mRNA is readily detectable in anoxic environments, *RAmy3D* expression is relatively small under aerobic conditions. Whereas, under AG, the level of soluble sugars drops, and sugar starvation induces the expression of *RAmy3D*, which helps in the production of α-amylase. *RAmy3D* expression is very important during the first 12-48 hours of AG, which helps in the breakdown of starch during the initial stages of germination (41). Overall factors influencing gene regulation and signalling pathways related to anaerobic germination tolerance (AGT) in rice are represented in Fig. 1.

Physiological and biochemical changes during AG

Starch, the principal carbon source that provides energy and primary products for rice germination, makes up 87.8% of the endosperm of rice. A study conducted by Zhang et al. (42) reported that starch in weedy rice is linked to better establishment of seedlings in AG. During AG, tolerant rice seeds undergo fermentative metabolism instead of mitochondrial respiration. Researchers noticed that in a tolerant variety grown in anaerobic environments, the expression levels of the mRNAs encoding pyruvate decarboxylase (PDC), aldehyde dehydrogenase (ALDH), and alcohol dehydrogenase 1 (ADH1) enzymes and their enzymatic activity were upregulated (43-44). Interestingly, Barik et al. (45), while studying native landraces,

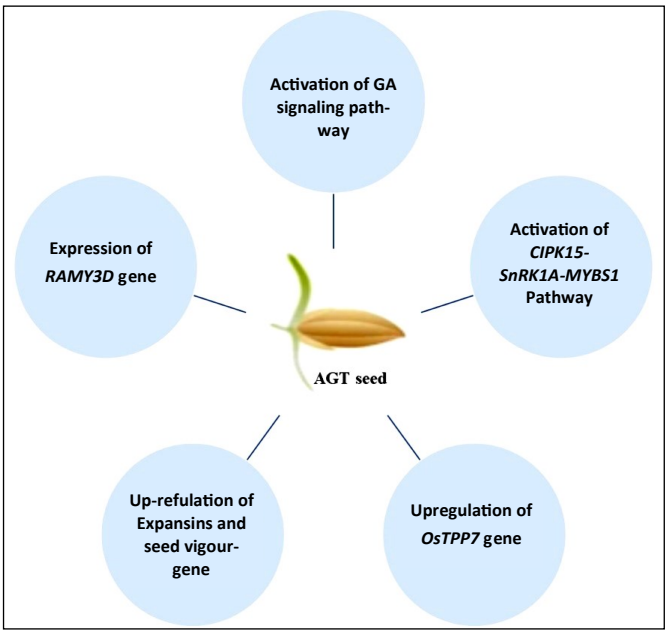

Fig 1. Factors influencing gene regulation and signalling pathway related to Anaerobic germination tolerance (AGT) in rice.

found that Bausaganthi, Patadhan, and Basantichudi maintained a higher sugar and starch content than susceptible cultivars and had higher activity of α-amylase and alcohol dehydrogenase, and demonstrated greater adaptive fitness for AG, which may be beneficial for improved seedling establishment underwater. In another study, it was found that tolerant genotypes were more resilient to low oxygen stress because they could continue to use their stored starch reserves due to increased amylase activity and absence of ethylene during the first 48 hours after sowing but did increase later on, with tolerant genotypes showing a greater increase in ethylene (13). Research also shows that there is a negative correlation between an increase in coleoptile length and poor growth of roots under anaerobic conditions (33). A summary of physiological and biochemical changes during AGT in rice is represented in Fig. 2.

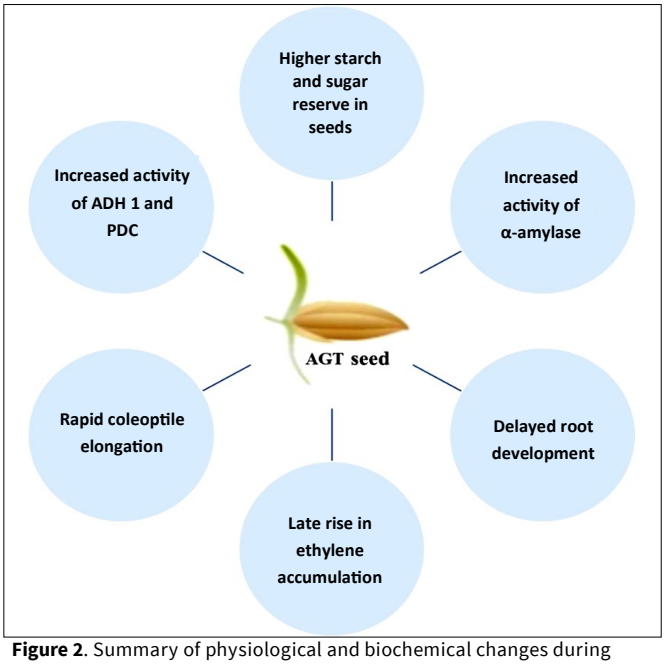

Figure 2. Summary of physiological and biochemical changes during anaerobic germination tolerance (AGT) in rice.

Quiescent strategy during the seedling stage

During the early 1950s several genotypes, mainly landraces, were screened for flooding and submergence tolerance. In the 1970s, flood-tolerant landraces were further screened at the International Rice Research Institute, Philippines, which resulted in the identification of a very good-tolerant genotype named Flood Resistant 13A (FR13A), which was initially collected from Odissa, India. At the seedling stage, FR13A showed decreased underwater shoot elongation, enabling them to endure total submersion brought on by flash flooding for 14 days(46). Xu and Mackill found that up to 70% of the phenotypic variance in tolerance FR13A was caused by a significant QTL SUBMERGENCE 1 (*SUB1*) on chromosome 9, and numerous functional studies have revealed that the ethylene response factor (ERF) transcription factor (TF), encoded by gene *SUB1A-1* found in the *SUB1* QTL, is the primary determinant of rice's quiescent strategy of submergence tolerance(47-48). Out of different ERF classes, Group VII ethylene response factors (ERF-VIIs) are engaged in hypoxic and submergence adaptation responses (in FR13A) through the regulation of the expression of transcription factor genes of *AP2/ERF* (APETALA2/Ethylene Response Factor). Three ERF genes, *SUB1A, SUB1B*, and *SUB1C,* are found at the *qSUB1* locus. Interestingly, *SUB1B* and *SUB1C* genes are present in every *O. sativa* variety that has qSUB1. *SUB1A* is responsible for the tolerance mechanism under submergence. The *SUB1* ERFs' phylogenetic analysis suggests that *SUB1A* originated from a duplication of *SUB1B,* presumably following the domestication of Indica rice (49-50).

There are two different allele forms for *SUB1A*: the *SUB1A-1* allele (FR13A) and the *SUB1A-2* allele (found in cultivars that are intolerant to submergence). The difference between the two alleles is only one amino acid substitution: serine in *SUB1A-1* becomes proline in *SUB1A-2.* As a result, only *SUB1A-1* can be phosphorylated(51-52). In response to submergence, *SUB1A-1* stimulates a rapid, sustained, and prominent accumulation of transcripts in the leaves of 14–28-day-old plants, while *SUB1A-2* stimulates a reduced amount of transcript induction by the stress(53-54).

When rice is submerged, endogenous ethylene accumulates. Plants that have accumulated ethylene induce the *SUB1A-1* gene expression, which then uses a negative feedback loop to limit the production of ethylene(55). The precursor of ET, 1-amino-1-propane carboxylic acid (ACC) may build up in an oxygen-deficient environment and impose negative feedback on the synthesis of GA. Gibberellic acid signalling repressors such as slender rice-1 (SLR1) and SLR1-like-1 (SLRL1) proteins accumulate more when the *SUB1A-1* allele is expressed, which limits gibberellic acid expression(56). Two ERF-VII TF-encoding genes, ERF66 and ERF67, have promoter regions that *SUB1A-1* TF binds to and activates. This results in significantly increased expression of these genes in *SUB1A-1*-introgressed cultivars under submergence. Subsequent research revealed that MPK3 phosphorylates *SUB1A-1* at Ser186 during submergence, increasing the protein's interaction with the ERF67

promoter. Furthermore, phospho-SUB1A-1 enlists the assistance of ADA2-GCN5 to alter the chromatin structure of the ERF67 promoter region, therefore triggering the expression of the ERF67 gene. During normal conditions, *ERF66* and *ERF67* are degraded through N-end rule proteolysis but stabilized only under hypoxic conditions and respond to flooding stress (57-58).

Under submergence, some of the brassinosteroid (BR) biosynthesis and signalling genes like *DWF 1*, *DWF4,* and *BZR3* are upregulated by *SUB1A-1,* which in turn enhances BR levels and BR signalling. Subsequently, BR stimulates the expression of GA 2-OXIDASE 7, a catabolic gene for GA, and raises the amounts of SLR1 protein, which downregulates GA synthesis. Brassinolide treatment of *SUB1A-1*-introgressed tolerant genotypes under control circumstances led to up-regulated *SUB1A-1* gene expression (56).

Key enzymes PDC and ADH catalyse alcoholic fermentation, which results in the conversion of pyruvic acid to ethanol and the maintenance of a restricted energy flow during submergence. ADH and PDC activities were reportedly higher in tolerant lines that had *SUB1A-1* introduced during submergence (57-58). Additionally, *SUB1A-1* lines accumulate reduced quantities of ethanol, lactate, and alanine as well as metabolic end-products of amino acid metabolism and limit the pace and extent of starch hydrolysis. Higher endogenous ethylene levels cause an ABA degradative enzyme to be produced, which lowers abscisic acid (ABA) levels. According to some research, rice plants submerged in water also exhibit a decrease in ABA content that is not dependent on the *SUB1A* gene, which reduces leaf senescence (59-60). A summary of gene regulation and signalling pathways of the quiescent strategy adopted during submergence in rice is shown in Fig. 3.

Several studies have reported important physiological and biochemical changes happening during submergence in the submergence tolerance genotypes (Fig. 4), *viz*., elevated non-structural carbohydrate reserve both before and after submergence, reduced internodal elongation, restrained leaf growth, inhibition of floral initiation, delayed dark-induced senescence, reduced chlorophyll degradation, and upregulation of antioxidant systems (61-64).

Numerous terrestrial plants have hydrophobic or water-repellent leaf surfaces that, when submerged, hold onto a tiny coating of air (gas film), which speeds up the process of underwater photosynthesis. Because of their hydrophobic surface, rice leaves initially hold onto gas films while submerged in water, but over time, this gas layer may thin and limit photosynthesis (65-67). The gene known as Leaf Gas Film 1 (*LGF1)*, discovered by Kurokaw et al. (68), is responsible for determining leaf gas films. The *LGF1* allele of hydroxysteroid dehydrogenase (*OsHSD1*) controls the amount of C30 primary alcohol and, consequently, the C30 primary alcohol-to-aldehyde ratio, which is crucial for the formation of abundant epicuticular wax platelets on rice leaves, which directly impacts surface hydrophobicity, gas film retention, and underwater photosynthesis during submergence. Chakraborty et al. (69) found that in the presence of *SUB1* QTL, *LGF* showed increased thickness of the *LGF* and hydrophobicity. Additionally, they reported that artificially eliminating the *LGF* led to a partial loss of tolerance, exhibiting elevated ethylene production and early induction of genes related to anoxia (*SUB1A-1, ACS5, Ramy3D, and ADH1*) and showed symptoms like faster breakdown of starch and chlorophyll, increased elongation of stems, and a partial loss of quiescence in rice genotypes containing *SUB1*. Overall, the discovery of *LGF1* provides an alternate mechanism for sub-

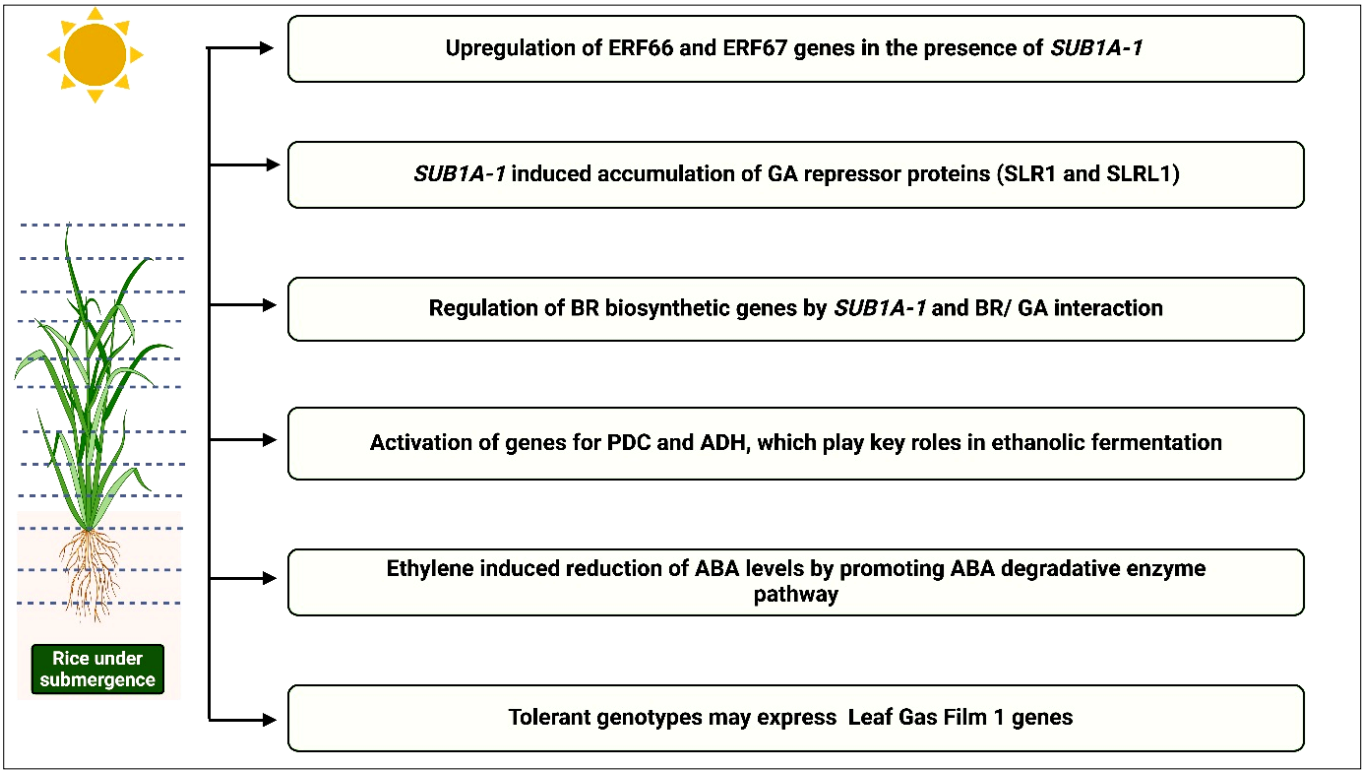

Fig 3. Summary of gene regulation and signalling pathway of quiescent strategy adopted during submergence in rice.

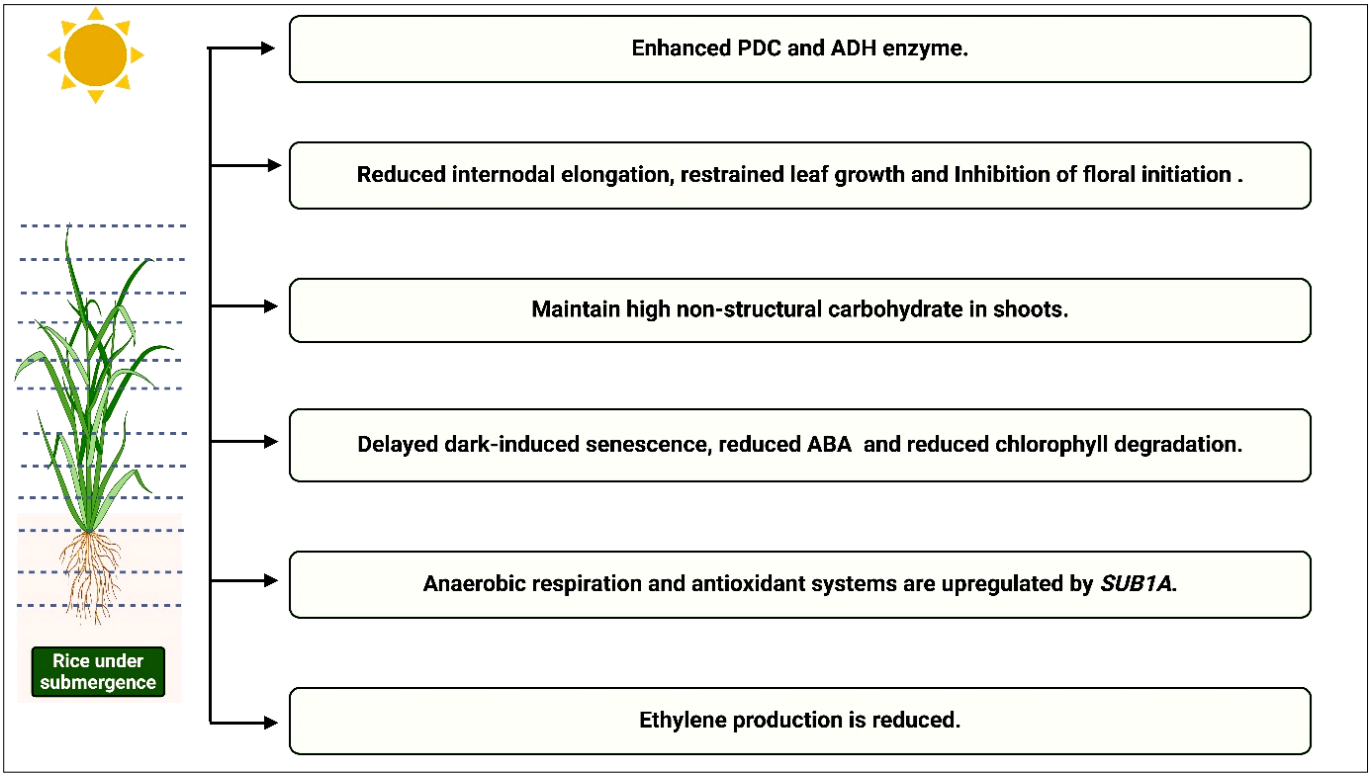

Fig 4. Summary of physiological and biochemical changes happening during submergence tolerance in rice.

mergence tolerance other than *SUB1A-1* and a deeper comprehension of the processes behind the reduction of ethylene-induced leaf senescence during submersion stress (16).

Escape strategy in deep-water rice

In deep-water ecology, rice grows normally in shallow water during the initial phase of growth. When the monsoon intensifies, water levels slowly rise. Under this circumstance, plants invest their energy into stem elongation for survival under rising water levels, which is called the escape strategy for deep-water rice (also known as floating rice) (70). Deepwater rice cultivars can grow up to 25 cm in height in a single day to stay in contact with light and air for photosynthesis (47). Under flooded conditions, the concentration of oxygen is rapidly decreased, and subsequently, carbon dioxide is increased. Along with this ethylene (ET), a gaseous phytohormone, is accumulated in higher concentrations in rice plants due to the activity of 1-Aminoacyclopropane 1-carboxylate synthase (ACS), a crucial enzyme in the route of ethylene production. Gibberellic acid (upregulation) and ABA production (down regulation) are regulated by ET, and GA subsequently promotes the expression of α- and β-expansin genes. Additionally, plants use non-structural carbohydrates and stored food for fast stem elongation. The expression of the SNORKEL1 and SNORKEL2 (SK1/SK2) genes, which are responsible for the expression of ERF transcription factors, is induced by the accumulated ET. These genes have a single AP2/ERF domain that initiates the synthesis of gibberellic acid and the ensuing internode elongation (70-72).

The gibberellin biosynthetic enzyme is encoded by the SEMIDWARF1 (SD1) gene, whose null allele results in a semidwarf phenotype. Plants with the deep-water rice-specific SD1 haplotype are activated after partial submersion by OsEIL1a, an ERF transcription factor, that results in internodal elongation. The enhanced synthesis of gibberellins, primarily GA4, which promotes internode elongation, is directed by the SD1 protein (GA20-oxidase for gibberellin production) (73). Recently, Nagai and Ashikari (74) reported that the accumulated GA upregulates the expression of *ACCELERATOR OF INTERNODE ELONGATION 1 (ACE1)*, the causal gene of *qLEI3*, (LEI = lowest elongated internode), and *ACE1* causes internode elongation by activating the intercalary meristem (IM) with GA. Furthermore, GA reduces the expression of the internode elongation repressor *PREMATURE INTERNODE ELONGATION 1* or *DECELERATOR OF INTERNODE ELONGATION 1 (PINE1/DEC1)*, the causal gene of *qLEI12*, resulting in a decrease in the repressive capacity of *PINE1/DEC1*, which initiates internode elongation in deep-water rice. The mechanism involved in deep-water rice upon partial submergence is depicted in Fig. 5.

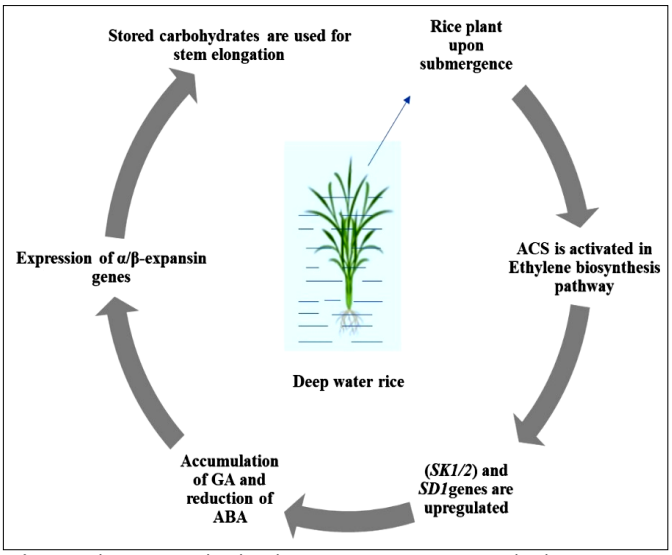

Fig 5. Mechanism involved in deep water rice upon partial submergence.

Role of aquatic adventitious roots in deep-water rice

In many species of wetland plants, adventitious roots are developed at the junction of stem nodes as a response to partial submergence. These roots are called aquatic adventitious roots (AAR), which remain floating in water rather than reaching the soil surface, and the main function of these roots is to acquire nutrition from flooded water (75-76). Recently, Lin et al. (77) reported QTL12, which harbours 17 genes, including *SK1/SK2*, promotes the development of an AAR system with greater developmental plasticity, which is highly adjusted to short-term, long-term, and recurrent flood events. They also found two types of roots; adventitious root 1 (AR1) developed within 3 days of submergence and adventitious root 2 (AR2) developed after 7 days. Both AR1 and AR2 showed differences in morphological and anatomical traits, and they concluded that AR2 is better adapted to long-term flooding than AR1 and also proposed that the AAR system functions as an evolutionary defence strategy to tackle periodic submergence (77).

Progress in identification of novel QTLs for submergence tolerance in rice

Identifying QTLs, or genes controlling tolerance for submergence, is a primary activity in plant breeding. The prominent QTLs identified further will be effectively incorporated into popular submergence susceptible varieties. To improve the tolerance, genetic studies have been conducted by many researchers to detect novel QTLs for submergence tolerance, AGT, flash flood tolerance, and escape from deep water using different germplasm sources and mapping populations. Angaji et al. (18) while mapping for tolerance to flooding during germination in rice, reported five putative QTLs, qAG-1-2, qAG-3-1, qAG-7-2, qAG-9-1, and qAG-9-2, explaining 17.9 to 33.5% of the phenotypic variation, among them, the QTL qAG-9-2 had the largest phenotypic variance (33.5%). Septiningsih et al. (78) identified the largest QTL on chromosome 7, named qAG7.1, derived from Ma-Zhan Red, which is one of the important QTL for AG. Later, a major QTL for AG was derived from Nanhi (AG tolerant line from India) named qAG7 on chromosome 7 with an LOD of 13.93 and explaining 22.3% of the phenotypic variation (79). Yang et al. (80) identified QTLs for rice resistance to AG using a biparental population and a high-density genetic bin map. They reported a total of 25 loci, in which 10 loci overlapped with previous reports, and obtained 12 promising candidate genes for AG. A novel QTL, named qACE3.1, has been identified on chromosome 3. This QTL is associated with the elongation of coleoptiles under anaerobic conditions and appears to have a particular impact on fermentative metabolism (80). Ghosal et al. (81) identified a total of four QTLs, which were located on chromosomes 1, 6, 7, and 10. Both qAG6-2 and qAG10-1 consistently appeared across various screening conditions and seedling ages. In another case, QTL mapping analysis was performed for 12 traits related to anaerobic seedling establishment during both germination and bud stages using the genotyping-by-sequencing (GBS) approach and identified a total of 20 loci. Within the identified loci, locus 3 underwent fine mapping. Through gene annotation and expression analysis data, a promising candidate gene, OsTPP1, was discovered (33). Thapa et al. (82), using a genome-wide association study (GWAS), found 30 significant GWAS QTLs, out of which 14 were colocalized with previously identified candidate genes of AG tolerance and 16 were potentially novel QTLs. Li et al. (83) reported 317 SNP loci for AG using the GWAS study, out of which 27 loci overlapped with the previously reported QTL physical locations. Furthermore, OsAlaAT1 on chromosome 10 located within the range of the GWAS location CVAN3d, associated with qAG10-1, is regarded as a more dependable candidate gene.

Breakthrough for identification of vegetative stage submergence tolerance, QTL began when Xu and Mackill identified a QTL called SUB1 for submergence tolerance from an indica rice variety FR13A on chromosome 9, which contributed 70% of the phenotypic variation for submergence tolerance (48). Later, Septiningsih et al. (78), based on their studies in a mapping population of IR 72 / Madabaru, reported three novel non-SUB1 QTLs, *viz*., qSUB1.1, qSUB2.1, and qSUB12.1, on chromosomes 1, 2, and 12, respectively. They suggested that an alternative pathway may exist in IR72 other than the one mediated by the *SUB1A* gene. This study inferred that the deployment of these novel QTLs along with SUB 1 can potentially enhance the submergence tolerance in flood-prone areas. Recently a new quantitative trait locus (QTL) has been reported and named qSUB2, located on chromosome 2, which is accountable for submergence tolerance in African rice (*Oryza glaberrima*), and the presence of qSUB2, when combined with SUB1A-1, enhances the submergence tolerance of rice (84-85).

Like AGT and flash flood tolerance, numerous attempts were also made to understand the genetics of deep -water stress tolerance in rice. The internode elongation in deep water rice is regulated by three QTLs on chromosomes 1, 3, and 12 (86-87). Hattori et al. (72) successfully identified a significant QTL denoted as qTIL12, associated with total internode elongation length, situated on chromosome 12. This QTL is responsible for the expression of Snorkel1 (SK1) and Snorkel2 (SK2), which play a crucial role in regulating the deep-water escape mechanism in rice. Later, Nagai et al. (74) detected two novel QTLs, qTIL2, and qTIL4, regulating deep-water response at the early leaf stage. Kuroha et al. (73) found that qTIL1 contains the SEMIDWARF1 (SD1) gene, which is involved in gibberellin biosynthesis and contributes to internode elongation during submergence. In a research investigation carried out by Lin et al. (77) an examination of previously documented deep-water QTLs revealed that qTIL1 and qTIL12 exhibited a notable enhancement in both the quantity of adventitious roots and their rate of growth. The summary of promising QTLs identified for submergence tolerance is listed in Table 1.

Breeding for submergence tolerance

Significant progress has been made in the development of submergence-tolerant rice cultivars in recent years, driven by the effective discovery and delineation of a QTL called

Table 1. List of promising QTLs identified for submergence tolerance in rice.

QTL	Chromo-some	Gene	Function	Reference
Promising QTL for Anaerobic germination				
qAG-9-2	9	*OsTPP7*/AG1	Sucrose synthesis and carbohydrate translocation to coleoptile under anoxia for rapid elongation of coleoptile	(18, 32)
qAG7.1	7	AG2	Submergence tolerance during the germination stage	(78, 82)
qAG2	2	*OsTPP1,*	Coleoptile response	(78, 75, 86)
qFCL-8	8	qAG-8-1	Flooding tolerance during germination	(18, 44, 82)
qNCL-1-2	1	qAG1-2	Anaerobic germination Index	(18, 82)
Promising QTL for vegetative stage submergence tolerance				
qSUB1 (Sub1)	9	*SUB1A*	Suppressed internode elongation, Chlorophyll degradation and carbohydrate consumption during submergence	(47, 50)
qSUB1.1	1		Submergence tolerance during the vegetative stage	(87)
LGF1	1	*OsHSD1*	Maintaining respiration and photosynthesis under submergence	(68)
Promising QTL for deep-water rice				
qTIL12	12	*SK1/ SK2*	Rapid Internode elongation during submergence	(72)
qTIL1	1	*SD1*	Higher gibberellin accumulation and internode elongation	(72, 73)
QTL12	12		Development of Aquatic adventitious roots (AAR)	(77)

AG: Anaerobic germination, **FCL** = Flooded coleoptile length, **NCL**= Normal coleoptile length, **LGF**= Leaf Gas Film 1, **TIL**: Total Internodal length.

SUBMERGENCE1. This QTL was originally discovered in the rice landrace FR13A. In addition to FR13A, the other landraces, such as FR43B from India, and Kurkaruppan, Goda Heenati and Thavalu from Sri Lanka, were reported to have tolerance to vegetative stage submergence. Similarly, major donors available for AG are Ma-Zhan Red (China), Nanhi (India), Kasalath (India), and Khao Hlan On (Myanmar). By involving these donors, many submergence -tolerant varieties have been developed and released for cultivation. Some of the tolerant mega varieties are IR64 *SUB1*, Swarna *SUB1*, Samba Mahsuri *SUB1*, CR1009 *SUB1*, BR11 *SUB1, CO43 SUB1,* and Thadokkam1 *SUB1.* Likewise, some of the AG-tolerant varieties are IR64-AG131, IR64-AG132, and CiherangAG1+SUB1 (8, 18, 88). The list of submergence-tolerant donors and varieties developed are represented in Table 2.

Table 2. List of donors and varieties developed for submergence tolerance.

Trait	Notable donors and varieties reported for submergence stress		Reference
Anaerobic germination	Donor	Ma-Zhan Red (China), Nanhi (India), Kasalath, (India), Khao Hlan On (Myanmar), Khaiyan (Bangladesh), Kalongchi (Bangladesh), Arroz da Terra (Japan), Koshihikari (Japan), Karuthakar, Poovan samba, Mattaikkar, Tulasi phula, Edakkal, and Manvilayan (India)	(18, 87, 88, 91,)
	Varieties developed	IR64-AG131, and IR64-AG132	(89)
Submergence tolerance	Donor	FR13A (India), Goda Heenati, Thavalu, and Kurkaruppan (Srilanka)	(13, 18, 89)
	Varieties developed	Swarna *SUB1*, CR1009 *SUB1,* CO 43 Sub1, IR64 *SUB1*, Samba Mahsuri *SUB1,* BR11 *SUB1,* Thadokkam1 *SUB1, CiherangAG1+SUB1,* and PSB-RC18	(68, 77)
Deep-water rice	Donor	Baisbish (Japan), and Rangdhakekua bao (India)	(89. 90)
	Varieties developed	Ambika, Saraswati, Sabita and Hangseswari (India)	(18, 74)

Conclusion and future prospects

Climate change is one of the important catastrophic events faced by humankind. It is expected that it is going to aggravate in the future. Agriculture in developing countries will be the most impacted by climate change. In order to sustain climate change, breeding climate-resilient crops like submergence-tolerant rice varieties is important. Understanding the different mechanisms involved in stage-specific submergence tolerance in rice helps us to develop better varieties. Moreover, identifying novel QTLs and donors tolerant to prolonged submergence is of prime importance in breeding for submergence tolerance. Short-term submergence poses challenges in rice production, especially in flood-prone areas. Many tolerant rice varieties conferring tolerance for a period of two weeks were developed through marker-assisted back cross-breeding. While the *SUB1* gene, identified in a tolerant variety FR13A, confers submergence tolerance for up to 2 weeks, longer-term submergence tolerance requires further investigations. At the International Rice Research Institute, Philippines, research initiatives are taken up to map genes or QTLs contributing to more than two weeks of submergence tolerance. Besides vegetative stage tolerance,

numerous attempts were made to understand anaerobic germination tolerance and deep-water stress tolerance. The QTLs for AGP were also deployed in developing rice varieties with AG. However, considering climate change and its impact on rice production, redeployment of breeding attempts to develop rice varieties tolerant to multiple abiotic stresses is important. In many rice ecologies, the combined effects of drought in the early phase of growth followed by submergence cause severe yield penalties. Therefore, the approach of simultaneous improvement of multiple abiotic stress tolerance becomes a key breeding strategy to develop climate-resilient rice varieties. Furthermore, it is also feasible to combine both abiotic and biotic stress-resistant genes through robust breeding designs and efficient phenotyping and genotypic tools. Through these means, rice varieties with various stress tolerance and preferred market qualities can be developed to address the future needs of the stakeholders while addressing climate-related challenges.

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Authors' contributions

The first draft of the manuscript was written by KM and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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