



# Mechanistic Insights and Genetic Approaches for Enhancing Submergence Tolerance in Rice

**Arya Bharti <sup>a</sup>, Ravi Kesari <sup>a\*</sup>, Sweta Sinha <sup>a\*</sup>,  
Sareeta Nahakpam <sup>b</sup>, Mankesh Kumar <sup>c</sup> and Chandan Roy <sup>d</sup>**

<sup>a</sup> Department of Molecular Biology and Genetic Engineering, BAC, BAU, Sabour, India.

<sup>b</sup> Department of Plant Physiology and Biochemistry, BAC, BAU, Sabour, India.

<sup>c</sup> Department of Plant Breeding and Genetics, BAC, BAU, Sabour, India.

<sup>d</sup> Department of Genetics and Plant Breeding, Agriculture University, Jodhpur, India.

## **Authors' contributions**

*This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.*

## **Article Information**

DOI: <https://doi.org/10.9734/jeai/2024/v46i82792>

### **Open Peer Review History:**

This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: <https://www.sdiarticle5.com/review-history/121547>

**Review Article**

**Received: 14/06/2024**

**Accepted: 17/08/2024**

**Published: 22/08/2024**

## **ABSTRACT**

Rice, a pivotal staple crop, serves as a dietary foundation for approximately half of the global population. Its cultivation, traditionally reliant on submerged conditions, faces significant challenges due to sudden flooding events. The majority of rice varieties are highly sensitive to prolonged submersion beyond a mere seven days, resulting in substantial yield losses. As global climate patterns shift, the occurrence and intensity of flooding are predictable to increase, exacerbating this issue. Therefore, development of rice varieties having enhanced submergence tolerance is critical

BAU COMMUNICATION NO. 1779/240729

\*Corresponding authors': E-mail: [kesariravi@gmail.com](mailto:kesariravi@gmail.com), [babylsweta@gmail.com](mailto:babylsweta@gmail.com);

**Cite as:** Bharti, Arya, Ravi Kesari, Sweta Sinha, Sareeta Nahakpam, Mankesh Kumar, and Chandan Roy. 2024. "Mechanistic Insights and Genetic Approaches for Enhancing Submergence Tolerance in Rice". *Journal of Experimental Agriculture International* 46 (8):1037-51. <https://doi.org/10.9734/jeai/2024/v46i82792>.

to sustaining productivity and ensuring food security in flood-prone regions. Understanding the physiological and biochemical mechanisms underlying submergence tolerance is crucial in this context. Key physiological mechanisms include the regulation of carbohydrate reserves for energy during low oxygen availability, ethylene-responsive factors, especially the Sub1A gene to, regulate growth and stress responses, curbing excessive elongation to conserve energy and enhance survival. Additionally, specialized tissues such as aerenchyma and adventitious roots improve oxygen transport and nutrient uptake under flooded conditions. Genetic approaches, including Marker-Assisted Selection (MAS), have been instrumental in the development of submergence-tolerant rice varieties. The integration of the Sub1 QTL, especially the Sub1A gene, into high-yielding rice varieties has led to significant advancements in breeding submergence-tolerant cultivars. These genetic improvements provide a promising solution to mitigate the detrimental effects of flooding on rice production, ensuring the stability and sustainability of this essential crop in the face of changing climate conditions. This review discusses various mechanisms adapted by rice and genetic advancements aimed at enhancing submergence tolerance in rice to secure food production for future generations.

*Keywords: Abiotic stress; MAS; QTL; Rice; Sub1; submergence tolerance.*

## 1. INTRODUCTION

Rice, which belongs to the poaceae family, is a staple crop globally, serving as the key food supply for more than half of the world's population, particularly in Asia, Latin America, Africa, and the Middle East [1-5]. Asia grows more than 90% of the world's total rice, significantly contributing to food security and development, especially in major rice-growing countries like China and India [1, 3-5]. Rice contains essential elements such as vitamin B6, selenium, and phosphorous, making it an important source of calories for billions of people worldwide [1, 2, 3-5]. Its growing area in India alone ranges from below sea level to high altitudes, demonstrating its adaptability and importance in many agro-climatic conditions [2]. Overall, rice is a cornerstone of world agriculture, providing food, nutrition, and a source of income for millions of people worldwide.

Drought, submergence, salt, heat, cold, acidity, and sodicity are all abiotic factors that have a significant impact on rice yield around the world [6, 7]. These stresses reduce agricultural production, affecting more than 90% of cultivated lands globally [6]. Abiotic stresses such as nutritional deficiency, heavy metals, salt, heat, and drought all contribute to a significant decrease in rice output under changing climatic conditions [8]. The predicted rise in rainfall variability, salinity and global temperatures will exacerbate the occurrence and severity of various abiotic stresses, affecting rice physiology and grain quality indexes [9]. Understanding the molecular and physiological mechanisms underlying productivity decline under these conditions is crucial for creating cultivars that can

withstand them while maintaining rice productivity [9]. Efforts to lessen these pressures include using microbes to alleviate abiotic stresses in rice, enhancing stress tolerance through molecular breeding, omics approaches, and contemporary biotechnology methods [6, 8,10].

Submergence is one of several abiotic stresses that can have a significant impact on rice yield, affecting plant height, chlorophyll content, and soluble sugar levels. Rice can undergo adaptive modifications to resist submergence stress, with some varieties displaying higher tolerance levels [11,12]. Rice adjusts to submergence via internal aeration and growth regulation. It produces aerenchyma and leaf gas films to facilitate aeration. Furthermore, several rice cultivars use growth control mechanisms to tolerate submergence, known as the quiescence or escape strategy. Research has demonstrated that the Submergence-1A (*SUB1A*) gene regulates the quiescence strategy, which is crucial for survival during flash floods. On the other hand, the SNORKEL1 (*SK1*) and SNORKEL2 (*SK2*) genes promote the escape strategy, which is necessary for surviving floods in deepwater [13]. Efforts to mitigate submergence effects have primarily focused on developing submergence-tolerant rice cultivars [14]. Understanding the molecular mechanisms behind submergence tolerance is crucial for increasing rice productivity under submergence conditions [15].

According to the research findings, improving rice submergence tolerance requires a variety of critical measures. One strategy is to modify particular genes, such as glucosyltransferase

gene *OsUGT75A*, which controls coleoptile length by lowering levels of jasmonic acid and abscisic acid during submergence [16]. Furthermore, the *SUB1A* gene, specifically the *SUB1A-1* allele, plays an important role in enhancing rice submergence tolerance by reducing ethylene synthesis and gibberellic acid response, conserving glucose storage, and activating stress-inducible gene expression [15,17]. Furthermore, strategies aimed at changing metabolism, starch metabolism, glycolytic flux, and sugar sensing can help overcome anoxic germination issues, increasing rice's ability to withstand submergence stress [18]. These combined genetic and metabolic approaches provide promising avenues for developing rice varieties with greater submergence tolerance for use in sustainable agricultural strategies.

## 2. SUBMERGENCE

Rice cultivation confronts substantial problems due to a wide range of abiotic stresses, such as submergence, waterlogging, drought, cyclones, and salinity. These stresses are often widespread throughout the year, with a heightened frequency during the kharif season. Among these factors, submergence stress provides a particularly pronounced hazard to rice plants, especially when they are subjected to oxidative stress. The predominance of submergence stress has severe repercussions for crop productivity. Despite its inherent tolerance to aquatic environments, the rice plant cannot grow when totally submerged in water for an extended duration [19]. Submergence reflects a sort of flooding stress that impairs plant performance at numerous levels, ultimately terminating in severe tissue damage and plant mortality. Rice crops submerged for longer than seven days inevitably succumb to this stress, with absolutely no possibility of recovery until the floodwaters recede. Submergence impacts crops in low-lying places, with two main environmental scenarios leading to submergence: rapid flooding and deepwater conditions. Flash flood submergence comprises a quick elevation of water levels, with plants remaining submerged for 1 to 2 weeks. In contrast, deepwater submergence entails water depths surpassing 100 cm, persisting for months [20]. Submergence can occur at any stage of rice growth, commencing with seed germination and continuing through maturity. In certain locations, periods of sluggish flooding are followed by abrupt flash floods, pushing farmers to produce

regionally adapted landraces that display resilience to this stress, even though they may yield less. Rice has adeptly evolved in environments prone to submergence through two key strategies: (i) submergence tolerance, which allows the plant to withstand sudden flash floods that result in partial to complete submersion for up to two weeks, and (ii) shoot elongation in deepwater environments (with water depths exceeding 100 cm), where water stagnation persists for several months and plant survival hinges on maintaining contact between the shoot and atmospheric oxygen. Under both submerged conditions, rice plants display numerous physiological, morphological, and biochemical responses. Notably, flood-intolerant types exhibit basic symptoms such as leaf senescence, necrosis, abscission, chlorosis, and lower survival rates [21]. The life of plants under submergence is greatly influenced by elements including oxygen and carbon dioxide concentrations, temperature, pH levels, turbidity, and water depth.

Modern high-yielding cultivars are quite vulnerable to submergence, even for just a few days. These factors can result in a significant decrease in production as a result of elevated death rates, limited tillering, and slow recovery [22-24]. In floodwater, the rate at which oxygen ( $O_2$ ) spreads decreases significantly, approximately 10,000 times less than in air. This obstruction hinders respiration and results in an energy deficit. This issue is mostly severe when the process of photosynthesis is decreased or completely absent because of the obstructed movement of  $CO_2$  and lack of sunlight. This results in mortality of plants during the submergence or soon after de-submergence [25-27]. Ethylene rises in plants after submergence due to heightened production and trapping when its diffusion is hindered by water. This subsequently induces submerged leaf senescence. Ethylene also induces faster loss of chlorophyll [28] in leaves of submerged plants by inducing gene expression level and enzymatic activity of chlorophyll breakdown enzyme chlorophyllase. This lowers the ability of  $CO_2$  fixation during and after submergence [29,30].

## 3. MECHANISM OF SUBMERGENCE TOLERANCE

Submergence tolerance is described as “the ability of a rice plant to survive 10–14 days of complete submergence and renew its growth when the water subsides” [31]. Submergence

tolerance in rice is a unique combination of adaptations that enable rice plants to live in regions prone to flooding and submersion. These adaptations span morphological, physiological, biochemical and genetic systems, each playing a critical part in the plant's ability to resist and recover from submergence. Following is the quick summary of the mechanism of submergence tolerance in rice.

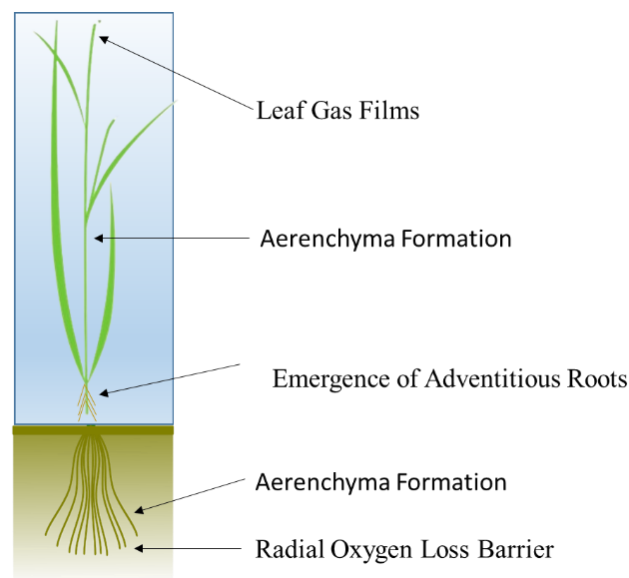
### 3.1 Morphological Adaptations

Morphological modifications contribute greatly to rice's submergence tolerance and include following features.

#### 3.1.1 Aerenchyma formation

Aerenchyma, a spongy tissue with vast intercellular spaces, facilitates efficient gas transfer between shoots and roots in rice. Aerenchyma formation in rice occurs under both aerobic and waterlogged conditions through different mechanisms (Fig. 1). Under aerobic conditions, rice forms constitutive aerenchyma. Recent discoveries highlight the role of auxin in this process, mediated by AUX/IAA and ARF signaling [32]. IAA13 and ARF19, highly up-regulated in the root cortex, co-regulate aerenchyma formation. When the LBD1-8, an LBD transcription factor controlled by an AUX/IAA-ARF complex, is overexpressed in the *iaa13* background, it restores aerenchyma formation, and application of auxin transport inhibitors prevents its formation, whereas natural

auxin reverses this effect [32]. Constitutive aerenchyma is linked to waterlogging tolerance, as seen in maize and wheat, which have limited waterlogging tolerance due to lack of constitutive aerenchyma [33, 34]. Aerenchyma development is increased in order to efficiently transport oxygen to the submerged roots and/or shoots when exposed to soggy environments [12, 33-35]. Inducible aerenchyma formation during waterlogged conditions is controlled by ethylene and reactive oxygen species (ROS) signaling pathways [35]. During waterlogging, ethylene rises in the tissue, triggering programmed cell death (PCD) and enhanced ethylene synthesis [34]. Ethylene promotes NADPH oxidase and RBOHH expression, leading to ROS formation, which results in PCD and aerenchyma production [34, 35]. Hypoxia induces CDPK5 and CDPK13 expression, which co-express with RBOHH, resulting in ROS accumulation and aerenchyma development [35]. Disruption of RBOH activity or inhibition of cytosolic calcium influx prevents the formation of aerenchyma formation by ethylene, emphasizing the significance of RBOHH. A recent study suggested that peroxynitrite (ONOO<sup>-</sup>) might also participate in ethylene-mediated aerenchyma development under waterlogging conditions [36]. Overall, aerenchyma formation in rice involves complex interactions between auxin, ethylene, and ROS signaling pathways, with constitutive aerenchyma aiding in aerobic conditions and inducible aerenchyma responding to waterlogged conditions to enhance plant survival and tolerance.



**Fig. 1. Anatomical and morphological adaptations in rice to submergence condition**

### 3.1.2 Effective barriers to radial oxygen loss

In roots, oxygen moves longitudinally via the aerenchyma and can be lost radially to the rhizosphere, a process known as radial oxygen loss (ROL) [26]. In order to adapt to this circumstance, rice plants respond to waterlogging by depositing lignin and suberin in the hypodermis and sclerenchyma of their roots, which forms a protective barrier [12, 34] (Fig. 1). Suberin, compared to lignin, is much more closely related to ROL barrier formation, as seen in rice mutants lacking suberin lamellae, which fail to block apoplastic tracer infiltration [37]. This barrier forms rapidly, with high resistance to O<sub>2</sub> diffusion observed within 6 hours of anoxia exposure and a complete barrier within 24 hours [38]. The formation of this barrier is triggered by compounds like H<sub>2</sub>S, Fe<sub>2</sub><sup>+</sup>, and carboxylic acids, produced by anaerobic bacteria in anoxic soils [39-41]. Transcriptomics indicates that genes implicated in suberin biosynthesis, such as *OsCYP86B3* and *OsABCG5*, are upregulated during flooding [37]. Additionally, ABA signal transduction is crucial for ROL barrier formation, as shown by impaired barriers in rice mutants with defective ABA biosynthesis [42]. A study done recently suggested that low nitrate condition under waterlogging may also involve in triggering exodermal suberization that creates a barrier to radial oxygen loss in rice roots [43]. The ROL barrier also restricts gas diffusion, including H<sub>2</sub>, water vapor, and H<sub>2</sub>S, and apoplastic movements of water, Na<sup>+</sup>, and Fe<sub>2</sub><sup>+</sup> [39, 44-46]. This multifunctional trait, combined with the formation of thick adventitious roots under soil flooding, conserves O<sub>2</sub> within the cortical tissues, optimizing root function in anoxic environments [47,48].

### 3.1.3 Leaf gas film

Underwater photosynthesis in rice is facilitated by its super-hydrophobic leaf cuticle, which preserves a thin gas film on the commencement of submergence (Fig. 1). This feature, prevents stomatal flooding and enhances gas exchange with the surrounding water, crucial for maintaining photosynthesis and respiration [49-51]. Rice achieves leaf hydrophobicity through multiple structural levels: the plicate leaf shape at the macro-level, micro-scale leaf papillae, and nano-scale wax platelets on the cuticle surface [52-55]. These gas films play a pivotal role in enhancing photosynthetic rates by facilitating rapid CO<sub>2</sub> diffusion to stomata and allowing O<sub>2</sub> produced during photosynthesis to diffuse into

the surrounding water [56]. However, the duration of these super-hydrophobic features is limited, typically disappearing in 4 to 7 days under field conditions, leading to reduced underwater net photosynthesis and accelerated chlorophyll degradation [57]. It has been found that the removal of leaf gas films artificially significantly decreases oxygen uptake and net photosynthetic rates, underscoring their critical role [50, 56, 58]. Mutants with decreased epicuticular wax lose their ability to retain gas films and sustain underwater photosynthesis after submergence, despite having usual leaf morphology [59]. These findings emphasize how leaf structural traits and genetic factors together support efficient underwater photosynthesis and respiration in submerged rice plants.

### 3.1.4 Adventitious root emergence

Adventitious roots (ARs) form a major part of the root system and emerge in response to waterlogging and submergence in rice [48, 60] (Fig. 1). These roots facilitate gas, water, and nutrient transport when soil-grown roots are oxygen-deprived. While cytokinin and auxin are essential for AR primordia formation [61], ethylene initiates their formation during submergence through coordinated signaling involving ROS, ethylene, and mechanical forces [62-64]. Genes of ethylene biosynthesis 1-Aminocyclopropane-1-Carboxylic Acid Oxidase 1 (*ACO1*) and *EOL1*, a BTB ubiquitin ligase, are highly expressed in epidermal cells situated above AR tips, increasing H<sub>2</sub>O<sub>2</sub> production and enhancing ethylene signaling by inhibiting the H<sub>2</sub>O<sub>2</sub> scavenger gene *MT2b* [63]. Ethylene also synergizes with gibberellin to induce AR formation, a process repressed by the application of exogenous ABA [65]. The absence of O<sub>2</sub> in submerged soils leads to soil root decay, highlighting the critical role of ARs in maintaining plant health under submerged conditions.

## 3.2 Physiological Mechanism

The physiological traits that are crucial for submergence tolerance in plants include minimizing elongation growth, maintaining high carbohydrate concentration, optimal rates of alcoholic fermentation, low sensitivity to ethylene or low synthesis of ethylene during submergence, and upregulation of antioxidant systems when water recedes. These features assist plants live in submergence circumstances and enable them to tolerate flooding. Some species of *Indica* are able to survive

submergence caused by flash floods by employing a distinctive "quiescent strategy." This strategy involves slowing down their growth in order to preserve essential carbohydrate reserves until the water recedes. Once the floodwaters have subsided, these stored carbohydrates are utilized for recovery and regeneration (Fig. 2). Periodic flooding throughout the rainy season is a common occurrence, leaving stagnant water up to 2 meters for several weeks. Deepwater rice has evolved an escape mechanism to adapt to this form of repeated flooding [31] (Fig. 2). In shallow water, deepwater rice grows normally, but when there is a significant rise in rainfall, it also rises taller. Deepwater rice types have the capacity to raise their height by around 25 cm per day as a strategy to dodge anoxic or hypoxic circumstances, enabling them to stay in touch with air and sunshine for photosynthesis [25, 66].

### 3.3 Biochemical Mechanism

Biochemical characteristics, such as glucose levels before and after submergence, are crucial variables for tolerance. Non-structural carbohydrates (NSC) are the primary source for energy synthesis in plants. Under complete submergence, NSC levels deplete rapidly [67]. Research on rice varieties with differing submergence tolerance revealed that submergence-tolerant landraces typically have higher NSC levels in their seedlings compared to susceptible varieties [68, 69]. The NSC reserves

are vital during submergence, supplying the energy necessary for growth and essential metabolic processes [70]. Interestingly, in a separate study, it was observed that there was no significant differences in glucose content before submergence between sensitive and tolerant genotypes [71]. Instead, a significant correlation was found between submergence tolerance and carbohydrate retention post-submergence [71]. In another study, it was found that initial NSC levels in dry seeds or 10-day-old seedling shoots before submergence did not consistently vary in submergence-tolerant varieties. However, these tolerant genotypes incline to utilize carbohydrates more slowly when submerged, potentially supplemented by energy from underwater photosynthesis, leading to reduced carbohydrate loss and quicker recovery after submergence [57, 67, 71, 72]. While some landraces and certain submergence-tolerant and deepwater landraces accumulate high carbohydrates in their shoots prior to submergence, this is not essential for surviving complete submergence [67].

Alcoholic fermentation is a critical metabolic pathway that provides the essential energy for seed germination in water and coleoptile elongation by improving glycolysis and ATP synthesis through  $NAD^+$  reuse. During alcohol fermentation, pyruvate is transformed into acetaldehyde by pyruvate decarboxylase and then into ethanol by the enzymatic activity of alcohol dehydrogenase [25, 73].

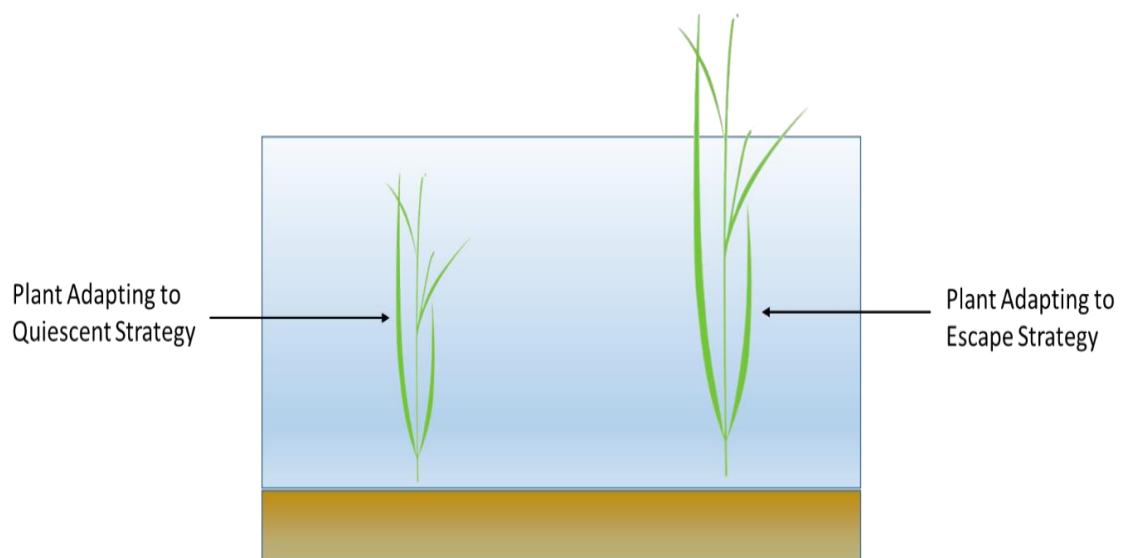


Fig. 2. Rice response to submergence condition through different strategies

Old leaves decay while the plant is submerged but regenerate quickly once the water recedes, aiding plant survival [21, 25]. In a study, it was discovered that both susceptible and tolerant cultivars had a substantial drop in chlorophyll content when exposed to submergence. Nevertheless, cultivars with tolerance managed to preserve higher chlorophyll levels both during the submersion phase and upon re-emergence [74]. Exposure of rice plants to submergence stress leads to the rapid accumulation of ROS such as superoxide ( $O_2^-$ ) and hydrogen peroxide ( $H_2O_2$ ). These ROS cause oxidative damage to lipids [75]. Plants have developed reactive oxygen scavenging systems that contain both antioxidant enzymes and non-enzyme antioxidants to battle free radicals and decrease damage caused by oxidative stress and ROS. Because the surrounding water contains molecular oxygen, the number of antioxidant enzymes rises in the submerged rice plant. Plants with high levels of antioxidant enzymes can tolerate oxidative stress [76]. During submergence, submergence-tolerant genotypes diminish their susceptibility to ethylene, a growth-regulating hormone, during submersion. This reduction inhibits excessive growth in the tough submergence conditions [30].

### 3.4 Genetic Regulation

Genetically, the submergence tolerance of rice is predominantly controlled by a quantitative trait locus (QTL) denoted as *Sub1*, which is situated on the chromosome nine with a LOD score of 36 and a  $R^2$  value of 69% [77]. This QTL, generated from the Aus variety Flood Resistant 13A (FR13A), provides great resilience to extended submersion. In contrast to the quiescent strategy demonstrated by FR13A, deepwater rice employs a unique survival strategy when confronted with season-long flooding. This includes the quick extension of its internodes to maintain touch with the air. This survival mechanism relies on a hereditary feature involving two key genes known as SNORKEL1 (*SK1*) and SNORKEL2 (*SK2*) [78]. These genes, identical to the *Sub1* locus, belong to the ERF family and are activated in response to stress imposed upon submergence and the plant hormone ethylene. When the plants are submerged, the restricted dispersion of ethylene promotes its buildup within the plant, leading to the activation of many members of *ERF* gene family, including *SK1*, *SK2*, *SUB1A*, and *SUB1C*, among others. Nonetheless, the fundamental processes that impact both *SUB1A* and

SNORKEL-related tolerance appear to rely on the plant hormone gibberellin (GA). GA has roles in several aspects of plant growth, development, and adaptability to stress [79]. Deepwater rice has high levels of GA, which result in the fast elongation of internodes and leaves. While the GA level in *SUB1A*-expressing plants hasn't been specifically documented, it has been suggested that alterations in the GA signaling pathway occur due to increased concentrations of GRAS family transcription factors known as SLENDER RICE1 (SLR1) and SLR1-Like1 (SLRL1) during submergence [80]. It was reported that the amount of SLR1 and SLRL1 protein rises when being submerged in submergence-tolerant *Sub1* introgressed rice but not in submergence-intolerant rice. These data imply that the limiting of growth as shown by submergence-tolerant rice is related to the buildup of SLR1 and SLRL1 through *SUB1A*.

Introgression of *Sub1A* into submergence-intolerant cultivars provides submergence tolerance [14, 81-83]. A marker-assisted backcrossing with the *Sub1A* gene resulting in six submergence-tolerant rice varieties, demonstrating significant potential for cultivation in places prone to flooding [14]. In a study undertaken to explore the influence of submergence and recovery on the growth and survival of *Sub1* near-isogenic lines (NILs) and FR13A under field circumstances, it was found that submergence considerably reduced biomass accumulation, especially in genotypes lacking *Sub1* [84]. This effect was more obvious when submergence persisted for 17 days. *Sub1* lines, on the other hand, exhibited higher chlorophyll content during submergence and had decreased loss of non-structural carbohydrates after submergence. During the recovery phase, genotypes missing *Sub1* showed quicker breakdown of chlorophyll. Interestingly, FR13A not only demonstrated slower leaf elongation after submergence but also acquired additional biomass. Additionally, FR13A displayed a higher recovery rate compared to *Sub1* lines. This suggests involvement of the additional genetic factors for submergence tolerance in FR13A with potential for further enhancing submergence tolerance by integrating these factors found in FR13A or other comparable landraces [85, 86].

In another study, the role of an UDP-glucosyltransferase gene (*OsUGT75A*) located within a significant QTL for rice coleoptile length during submergence was examined. It was discovered that *OsUGT75A* has the ability to

glycosylate ABA and JA, resulting in a decrease in the levels of free ABA and JA, respectively. This, in turn, promotes the growth of rice coleoptiles in submerged conditions. Therefore, *OsUGT75A* could be a valuable target for breeding rice varieties that are well-suited for direct seeding cultivation [16].

#### 4. GENETIC APPROACHES FOR ENHANCING SUBMERGENCE TOLERANCE RICE

Genetic approaches for enhancing submergence tolerance in rice involve various strategies. Marker-assisted selection, which is one of the contemporary breeding techniques has been utilized to introgress submergence-tolerant QTLs Sub1 into many high yielding rice varieties, showing promising results in developing submergence-tolerant varieties [14, 83]. Genetic engineering has also been shown to be a promising strategy for developing submergence tolerant rice.

##### 4.1 Marker-Assisted Breeding of SUB1 QTL

Marker-assisted breeding is a useful technique that uses DNA-based molecular markers closely associated with desirable traits to speed up phenotype screening. Marker-assisted backcrossing (MABC) is one of the major applications of marker-assisted breeding. The main principle of MABC is to selectively transfer a particular allele situated at the target locus from a donor line to a recipient line, and taking precautions to prevent the inadvertent incorporation of donor genetic information into other regions of the genome. Molecular markers have an important role in expediting the selection process, resulting in greater genetic gains in less time. This method was particularly effective in maximizing the potential of QTLs with significant implications, such as Sub1 in rice breeding programs. It employs a variety of selections, including foreground, recombinant, and background selection, which use molecular markers that are tightly associated with Sub1, around Sub1, or unrelated to Sub1. As stated previously, Sub1's ability to transfer submergence tolerance has been confirmed in studies from diverse genetic backgrounds, significantly improving rice survival during submergence and productivity under flash flood conditions.

In one significant study, the Sub1 QTL from FR13A-derived lines was successfully transplanted into four major rice varieties: Samba Mahsuri, CR1009, IR64, and Thadokkham 1 [14]. This method used the gene-specific marker ARTS for foreground selection, while recombinant selection used RM8300 and several SSR markers located upstream of RM8300. Background selection, utilizing a total of 53 polymorphic markers encompassing all chromosomes, enabled the achievement of an individual plant with the Sub1 locus in BC<sub>3</sub>F<sub>1</sub> while keeping a genetic background consisting of 98.6% recurrent parents. In another study, a modified MABC approach was used to introgress Sub1 into the rice variety Ranjit with speed and precision [87]. This involved using gene-based markers Sub1BC<sub>2</sub> and 50051 SNPs for foreground and background selection during backcrosses between Ranjit and the Sub1 donor, Swarna-Sub1. Ranjit-Sub1, developed through selection in the BC<sub>2</sub>F<sub>2</sub> generation, displayed submergence tolerance comparable to the tolerant donor parent while achieving a background recovery of 96.54%. Similarly, marker-assisted backcross was used to improve submergence tolerance and grain yield in the Maudamani rice variety [88]. Progenies harboring both Sub1 and GW5 QTLs were chosen via foreground and background screening, significantly increasing the recipient parent's genome recovery in the BC pyramided line by up to 96.875% while maintaining consistency in several morphological and qualitative characteristics. Sub1 has been introduced into many rice mega-varieties. In India, for example, rice varieties such as Swarna Sub-1 and Samba Masuri Sub-1 have been created as flood-tolerant variants of the popular mega-variety Swarna (MTU 7029) and Samba Masuri (BPT-5204) [24, 83]. The experimental evidence has shown that under submergence conditions, these stress-tolerant varieties of rice significantly yielded higher than their traditional equivalents. In flood-prone lowlands of Odisha, India, the Swarna Sub-1 rice variety has been reported to produce yields up to 45% higher than the traditional varieties it replaced [89]. A field survey conducted in the northeastern region of Uttar Pradesh revealed that submergence-tolerant rice varieties had a 39% higher yield and generated 63% greater net returns compared to other commonly grown varieties in the area [90].

Apart from the Sub1 QTL, various other QTLs have also been identified for submergence tolerance, some of which are listed in Table 1.



**Table 1. List of some of the QTLs identified for submergence tolerance others than Sub1 QTL**

| S. No. | QTL Name       | Parents  | Phenotypic Variation ( $R^2$ )                          | References |
|--------|----------------|--|---|------------|
| 1.     | qSUB2          | 'TOS6454' (Moderately submergence-tolerant) and 'FARO44', 'FARO52', 'FARO60' (submergence susceptible) | 27.7%   | [91]       |
| 2.     | <i>qSUB1</i>   | 165 RILs derived from crosses between 'Milyang 23' and 'Tong 88-7'                                     | 9.44%   | [92]       |
| 3.     | <i>qSUB3</i>   |  | 14.62%  |            |
| 4.     | <i>qSUB4</i>   |  | 9.74%   |            |
| 5.     | <i>qSUB7</i>   |  | 7.09%   |            |
| 6.     | <i>qCL-1.1</i> |  | 272 RILs from crosses between 'Luohui 9' and 'RPY geng' |            |
| 7.     | <i>qCL-3.1</i> |  | 8.81%   |            |
| 8.     | qSUB1.1        | F <sub>2:3</sub> population between 'IR72' and   | 52.3%   | [94]       |
| 9.     | qSUB2.1        | 'Madabaru'   | 36.4%   |            |
| 10.    | qSUB9.1        |  | 17.1%   |            |
| 11.    | qSUB12.1       |  | 16.3%   |            |

#### 4.2 Genetic Engineering for Enhancing Submergence Tolerance Rice

By employing transgenic technology, the functionality of various genes involved in diverse processes for enhanced submergence tolerance has been attempted not only in various model systems but also in rice, which has paved the way for the development of transgenic rice. Transgenic approaches have shown promising results in developing submergence-tolerant rice by modifying the expression of specific genes. Overexpression of the pyruvate decarboxylase gene (*PDC1*) in transgenic rice enhanced metabolic capacity under anaerobic conditions, leading to increased ethanol formation and survival rates afterward submergence [95]. Overexpression of *bZIP72*, which was found to be induced by submergence, increased the germination of seeds and elongation of coleoptiles in submerged rice. Remarkably, it was found that *bZIP72* directly interacts with the promoter region of alcohol dehydrogenase 1 (*ADH1*), boosting its functionality and resulting in increased production of NAD<sup>+</sup>, NADH, and ATP. These metabolites play crucial roles in the alcoholic fermentation and glycolysis pathway, ultimately generating essential energy reserves that confer tolerance to submergence [96]. Similarly, transgenic rice overexpressing *OsARD1*, which is implicated in the ethylene biosynthesis pathway, exhibits enhanced submergence tolerance, decreased sensitivity to drought and salt stresses, and increased ethylene content, promoting shoot elongation to escape submergence [97]. Furthermore, knocking out the *SAB23* gene, which encodes a PHD-type transcription factor that negatively

regulates submergence tolerance, results in improved submergence resilience by modulating gibberellin levels [98]. In addition to the aforementioned genes, numerous more genes have been demonstrated to confer submergence tolerance in plant species other than rice. The overexpression of *Vitreoscilla* haemoglobin (*VHb*) in cabbage (*Brassica oleracea* var. *Cabitata*), which acts as a carrier and transporter of oxygen, showed tolerance to a prolonged submergence treatment [99]. Researchers are focusing on plant cysteine oxidase and its interaction with ERF-VII to enhance submergence tolerance. Plant cysteine oxidases (PCOs) are enzymes in plants that sense oxygen levels and catalyze the oxygen-dependent step that initiates the degradation of Group VII ethylene response transcription factors (ERF-VIIs) through the N-degron pathway [100]. Completely suppressing the production of PCO is crucial for the plants. As inhibiting the PCO entirely is critical for the plants, CRISPR-mediated base editing may be a suitable approach to manipulate their O<sub>2</sub> sensitivity and/or substrate specificity for stabilizing ERF-VII for improved submergence tolerance [100]. These studies collectively highlight the potential of transgenic technologies in enhancing submergence tolerance in rice, paving the way for the development of resilient rice cultivars.

#### 5. CONCLUSION

The significance of rice as a staple crop cannot be emphasized, considering its important role in global food security, especially in Asia, where it forms the dietary foundation for billions. However, rice productivity is severely threatened

by abiotic difficulties, particularly submergence, which results in significant yield losses. Submergence stress damages rice plants' physiological, morphological, and biochemical stability, resulting in reduced growth and high mortality. Advances in understanding the molecular mechanisms behind submergence tolerance, such as the role of the *SUB1A* and *SNORKEL* genes, have paved the way for the development of rice cultivars that can withstand such stresses. These genetic findings, combined with morphological, physiological, and biochemical adaptation strategies, are critical for increasing rice resilience and ensuring food security.

## 6. FUTURE PROSPECTUS

Future research should focus on integrating sophisticated biotechnological technologies, such as CRISPR-Cas9 gene editing, with traditional breeding strategies to increase submergence tolerance in rice. Exploring the synergistic impact of combining diverse stress-tolerance genes and understanding the intricate regulatory networks driving these features will be crucial. Additionally, widening the study to encompass the influence of climate change on submergence stress and constructing prediction models to guide adaptive agricultural approaches can further safeguard rice production. Collaborative efforts between scientists, farmers, and policymakers will be important to adopting these technologies on a worldwide scale, ensuring sustainable rice cultivation in the face of mounting environmental issues.

## DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

## COMPETING INTERESTS

Authors have declared that no competing interests exist.

## REFERENCES

1. Al-Hashimi AM. A review: Growing rice in the controlled environments. *Biosci. Biotechnol. Res. Asia*. 2023;20(1):13-28.
2. Theerthana T, Fathima P, Denesh G, Prakash S, Asha N. Influence of irrigation management practices and different establishment methods on nutrient use efficiency of rice. *Int J Curr Microbiol Appl Sci*. 2020;9(11):3213-323.
3. Maurya B, Singh P, Verma O, Mandal D. Genetic variability and divergence analysis in rice (*Oryza sativa* L.) under sodic soil. *Int J Curr Microbiol Appl Sci*. 2017;6(10):2865-69.
4. Trivedi VK, Pandey M, Chauhan GV, Tomer R, Trivedi A. Effect of the Nutrients on Yield and Yield Attributing Characters in Rice Crop. *Int J Curr Microbiol App Sci*. 2018;7(5):1958-64.
5. Kanwar S, Nag Y. To study correlation and path analysis in rice breeding lines. *Int J Curr Microbiol Appl Sci*. 2019;8: 2481-7.
6. Kumar U, Kaviraj M, Kundu S, Rout S, Priya H, Nayak A. Microbial alleviation of abiotic and biotic stresses in rice. In: Singh NK, Chattopadhyay A, Lichtfouse E, editors. *Sustainable Agriculture Reviews 60: Microbial Processes in Agriculture*: Springer. 2023;243-68
7. Ismail AM, Singh US, Singh S, Dar MH, Mackill DJ. The contribution of submergence-tolerant (Sub1) rice varieties to food security in flood-prone rainfed lowland areas in Asia. *Field Crops Res*. 2013;152:83-93.
8. Radha B, Sunitha NC, Sah RP, TP MA, Krishna G, Umesh DK et al. Physiological and molecular implications of multiple abiotic stresses on yield and quality of rice. *Front. Plant Sc*. 2023; 13:996514.
9. Rasheed R, Ashraf MA, Hussain I, Ali S, Riaz M, Iqbal M, et al. Varietal Physiology, Metabolic Regulation, and Molecular Responses of Rice Genotypes to Diverse Environmental Stresses. In: Roychoudhury A, Aftab T, Acharya K, editors. *Omics Approach to Manage Abiotic Stress in Cereals*: Springer. 2022;321-39.
10. Syed M, Ahmed M, Debsharma S, Jahan N, Afrin W, Biswas A, et al. Breeding and omics approaches to understand abiotic stress response in rice. In: Roychoudhury A, Aftab T, Acharya K, editors. *Omics Approach to Manage Abiotic Stress in Cereals*: Springer; 2022. p. 341-404.
11. Phukan UJ, Jindal S, Laldinsangi C, Singh PK, Longchar B. A microscopic scenario on recovery mechanisms under waterlogging and submergence stress in rice. *Planta*. 2024;259(1):9.

12. Nishiuchi S, Yamauchi T, Takahashi H, Kotula L, Nakazono M. Mechanisms for coping with submergence and waterlogging in rice. *Rice*. 2012;5:1-14.
13. Bashar KK, Tareq MZ, Amin MR, Honi U, Tahjib-Ul-Arif M, Sadat MA et al. Phytohormone-mediated stomatal response, escape and quiescence strategies in plants under flooding stress. *Agronomy*. 2019;9(2):43.
14. Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S et al. Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. *Ann. Bot.* 2009;103(2):151-60.
15. Amjad I, Kashif M, Dilshad R, Javed MA, Aziz S, Khalid MN et al. Submergence tolerance regulator, SUB1a: convergence of submergence and drought response pathways in rice. *Journal of Global Innovations in Agricultural Sciences*. 2022;10(4):191-199.
16. He Y, Sun S, Zhao J, Huang Z, Peng L, Huang C et al. UDP-glucosyltransferase OsUGT75A promotes submergence tolerance during rice seed germination. *Nat. Commun.* 2023;14(1):2296.
17. Lin C-C, Lee W-J, Zeng C-Y, Chou M-Y, Lin T-J, Lin C-S et al. SUB1A-1 anchors a regulatory cascade for epigenetic and transcriptional controls of submergence tolerance in rice. *PNAS Nexus*. 2023;2(7):pgad229.
18. Adak MK, Das A, Kundu A, Chatterjee M, Hasanuzzaman M. Molecular Mechanisms in Understanding Anoxia Tolerance in Rice Seeds under Submergence and Their Implication in Rice Biotechnology. *Seeds*. 2023;2(3):246-58.
19. Ito O, Ella E, Kawano N. Physiological basis of submergence tolerance in rainfed lowland rice ecosystem. *Field Crops Res*. 1999;64(1-2):75-90.
20. Kannan E, Paliwal A, Sparks A. Spatial and temporal patterns of rice production and productivity. In: Mohanty S, Chengappa PG, Mruthyunjaya, Ladha JK, Baruah S, Kannan E, et al., editors. *The Future Rice Strategy for India*: Elsevier. 2017;39-68.
21. Sarkar R, Reddy J, Sharma S, Ismail AM. Physiological basis of submergence tolerance in rice and implications for crop improvement. *Curr. Sci*. 2006;899-906.
22. Ismail A, Thomson M, Singh R, Gregorio G, Mackill D. Designing rice varieties adapted to coastal areas of South and Southeast Asia. *J Indian Soc Coast Agric Res*. 2008;26:69-73.
23. Singh S, Mackill DJ, Ismail AM. Responses of SUB1 rice introgression lines to submergence in the field: yield and grain quality. *Field Crops Res*. 2009;113(1):12-23.
24. Singh U, Dar M, SINGH S, Zaidi N, Bari M, Mackill D et al. Field performance, dissemination, impact and tracking of submergence tolerant (Sub1) rice varieties in South Asia. *SABRAO J. Breed. Genet*. 2013;45(1).
25. Bailey-Serres J, Voeselek L. Flooding stress: acclimations and genetic diversity. *Annu Rev Plant Biol*. 2008;59:313-39.
26. Jackson MB, Ram PC. Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. *Ann. Bot.* 2003;91(2):227-41.
27. Licausi F, Perata P. Low oxygen signaling and tolerance in plants. *Adv. Bot. Res*. 2009;50:139-98.
28. Jackson M, Waters I, Setter T, Greenway H. Injury to rice plants caused by complete submergence; a contribution by ethylene (ethene). *J. Exp. Bot.* 1987;38(11):1826-38.
29. Sone C, Sakagami JI. Physiological mechanism of chlorophyll breakdown for leaves under complete submergence in rice. *Crop Sci*. 2017;57(5):2729-38.
30. Ella E, Kawano N, Yamauchi Y, Tanaka K, Ismail A. Blocking ethylene perception during submergence reduced chlorophyll degradation and improved seedling survival in rice. *Funct. Plant Biol*. 2003;30(7):813-9.
31. Catling D. Rice in deep water. Growth and development. *International Rice Research Institute P*. 1992:121-69.
32. Yamauchi T, Tanaka A, Inahashi H, Nishizawa NK, Tsutsumi N, Inukai Y et al. Fine control of aerenchyma and lateral root development through AUX/IAA-and ARF-dependent auxin signaling. *Proc. Natl. Acad. Sci. U.S.A.* 2019;116(41):20770-5.
33. Colmer T, Voeselek L. Flooding tolerance: suites of plant traits in variable environments. *Funct. Plant Biol*. 2009;36(8):665-81.
34. Yamauchi T, Colmer TD, Pedersen O, Nakazono M. Regulation of root traits for

- internal aeration and tolerance to soil waterlogging-flooding stress. *Plant Physiol.* 2018;176(2):1118-30.
35. Yamauchi T, Yoshioka M, Fukazawa A, Mori H, Nishizawa NK, Tsutsumi N et al. An NADPH oxidase RBOH functions in rice roots during lysigenous aerenchyma formation under oxygen-deficient conditions. *Plant Cell.* 2017;29(4):775-90.
  36. Singh P, Jaiswal S, Kushwaha A, Gahlowt P, Mishra V, Tripathi DK et al. Peroxynitrite is essential for aerenchyma formation in rice roots under waterlogging conditions. *Planta.* 2023;258(1):2.
  37. Shiono K, Ando M, Nishiuchi S, Takahashi H, Watanabe K, Nakamura M et al. RCN1/OsABCG5, an ATP-binding cassette (ABC) transporter, is required for hypodermal suberization of roots in rice (*Oryza sativa*). *Plant J.* 2014;80(1):40-51.
  38. Shiono K, Ogawa S, Yamazaki S, Isoda H, Fujimura T, Nakazono M et al. Contrasting dynamics of radial O<sub>2</sub>-loss barrier induction and aerenchyma formation in rice roots of two lengths. *Ann. Bot.* 2011;107(1):89-99.
  39. Peralta Ogorek LL, Takahashi H, Nakazono M, Pedersen O. The barrier to radial oxygen loss protects roots against hydrogen sulphide intrusion and its toxic effect. *New Phytol.* 2023;238(5):1825-37.
  40. Mongon J, Konnerup D, Colmer TD, Rerkasem B. Responses of rice to Fe<sup>2+</sup> in aerated and stagnant conditions: growth, root porosity and radial oxygen loss barrier. *Funct. Plant Biol.* 2014;41(9):922-9.
  41. Colmer TD, Kotula L, Malik AI, Takahashi H, Konnerup D, Nakazono M et al. Rice acclimation to soil flooding: low concentrations of organic acids can trigger a barrier to radial oxygen loss in roots. *Plant Cell Environ.* 2019;42(7):2183-97.
  42. Shiono K, Yoshikawa M, Kreszies T, Yamada S, Hojo Y, Matsuura T et al. Abscisic acid is required for exodermal suberization to form a barrier to radial oxygen loss in the adventitious roots of rice (*Oryza sativa*). *New Phytol.* 2022;233(2):655-69.
  43. Shiono K, Ejiri M, Sawazaki Y, Egishi Y, Tsunoda T. Low nitrate under waterlogging triggers exodermal suberization to form a barrier to radial oxygen loss in rice roots. *Plant Physiol.* 2024:kiae278.
  44. Peralta Ogorek LL, Pellegrini E, Pedersen O. Novel functions of the root barrier to radial oxygen loss—radial diffusion resistance to H<sub>2</sub> and water vapour. *New Phytol.* 2021;231(4):1365-76.
  45. Krishnamurthy P, Ranathunge K, Nayak S, Schreiber L, Mathew M. Root apoplastic barriers block Na<sup>+</sup> transport to shoots in rice (*Oryza sativa* L.). *J. Exp. Bot.* 2011;62(12):4215-28.
  46. Jiménez JdlC, Pellegrini E, Pedersen O, Nakazono M. Radial oxygen loss from plant roots—methods. *Plants.* 2021;10(11):2322.
  47. Pedersen O, Sauter M, Colmer TD, Nakazono M. Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytol.* 2021;229(1):42-9.
  48. Lorbiecke R, Sauter M. Adventitious root growth and cell-cycle induction in deepwater rice. *Plant Physiol.* 1999;119(1):21-30.
  49. Raskin I, Kende H. How does deep water rice solve its aeration problem. *Plant Physiol.* 1983;72(2):447-54.
  50. Colmer T, Pedersen O. Oxygen dynamics in submerged rice (*Oryza sativa*). *New Phytol.* 2008;178(2):326-34.
  51. Pedersen O, Herzog M. The Importance of Leaf Gas Films for Gas Exchange During Submergence. In: Sakagami J-I, Nakazono M, editors. *Responses of Plants to Soil Flooding*: Springer; 2024. p. 89-101.
  52. Bhushan B, Jung YC, Koch K. Micro-, nano-and hierarchical structures for superhydrophobicity, self-cleaning and low adhesion. *Philos. Trans. R. Soc. A.* 2009;367(1894):1631-72.
  53. Ensikat HJ, Ditsche-Kuru P, Neinhuis C, Barthlott W. Superhydrophobicity in perfection: the outstanding properties of the lotus leaf. *Beilstein J. Nanotechnol.* 2011;2(1):152-61.
  54. Koch K, Barthlott W. Superhydrophobic and superhydrophilic plant surfaces: an inspiration for biomimetic materials. *Philos. Trans. R. Soc. A.* 2009;367(1893):1487-509.
  55. Herzog M, Konnerup D, Pedersen O, Winkel A, Colmer TD. Leaf gas films contribute to rice (*Oryza sativa*) submergence tolerance during saline floods. *Plant Cell Environ.* 2018;41(5):885-97.
  56. Pedersen O, Rich SM, Colmer TD. Surviving floods: leaf gas films improve O<sub>2</sub> and CO<sub>2</sub> exchange, root aeration, and growth of completely submerged rice. *Plant J.* 2009;58(1):147-56.

57. Winkel A, Pedersen O, Ella E, Ismail AM, Colmer TD. Gas film retention and underwater photosynthesis during field submergence of four contrasting rice genotypes. *J. Exp. Bot.* 2014;65(12):3225-33.
58. Colmer TD, Winkel A, Pedersen O. A perspective on underwater photosynthesis in submerged terrestrial wetland plants. *AoB Plants.* 2011;2011:plr030.
59. Kurokawa Y, Nagai K, Huan PD, Shimazaki K, Qu H, Mori Y et al. Rice leaf hydrophobicity and gas films are conferred by a wax synthesis gene (LGF 1) and contribute to flood tolerance. *New Phytol.* 2018;218(4):1558-69.
60. Steffens B, Rasmussen A. The physiology of adventitious roots. *Plant Physiol.* 2016;170(2):603-17.
61. Meng F, Xiang D, Zhu J, Li Y, Mao C. Molecular mechanisms of root development in rice. *Rice.* 2019;12(1):1.
62. Steffens B, Sauter M. Epidermal cell death in rice is regulated by ethylene, gibberellin, and abscisic acid. *Plant Physiol.* 2005;139(2):713-21.
63. Steffens B, Sauter M. Epidermal cell death in rice is confined to cells with a distinct molecular identity and is mediated by ethylene and H<sub>2</sub>O<sub>2</sub> through an autoamplified signal pathway. *Plant Cell.* 2009;21(1):184-96.
64. Steffens B, Kovalev A, Gorb SN, Sauter M. Emerging roots alter epidermal cell fate through mechanical and reactive oxygen species signaling. *Plant Cell.* 2012;24(8):3296-306.
65. Steffens B, Wang J, Sauter M. Interactions between ethylene, gibberellin and abscisic acid regulate emergence and growth rate of adventitious roots in deepwater rice. *Planta.* 2006;223:604-12.
66. Vergara B, Jackson B, De Datta S. Deep water rice and its response to deep water stress. *Proceedings of the Symposium on Climate & Rice.* International Rice Research Institute; 1976. p. 301-19.
67. Das KK, Sarkar RK, Ismail AM. Elongation ability and non-structural carbohydrate levels in relation to submergence tolerance in rice. *Plant Sci.* 2005;168(1):131-6.
68. Chaturvedi G, Ram P, Singh A, Ram P, Ingram K, Singh B, et al. Carbohydrate status of rainfed lowland rices in relation to submergence, drought and shade tolerance. In: Singh V, Singh R, Singh B, Zeigler R, editors. *Physiology of stress tolerance in plants* International Rice Research Institute, Los Banos; 1996. p. 103-22.
69. Sarkar R. Saccharide content and growth parameters in relation with flooding tolerance in rice. *Biol. Plant.* 1997;40:597-603.
70. Sarkar RK, De R, Reddy J, Ramakrishnaya G. Studies on the submergence tolerance mechanism in relation to carbohydrate, chlorophyll and specific leaf weight in rice (*Oryza sativa* L.). *J Plant Physiol.* 1996;149(5):623-5.
71. Mazaredo A, Vergara B. Physiological differences in rice varieties tolerant of and susceptible to complete submergence. *Proceedings of the 1981 international deepwater rice workshop.* International Rice Research Institute; 1982. p. 327-41.
72. Winkel A, Colmer TD, Ismail AM, Pedersen O. Internal aeration of paddy field rice (*Oryza sativa*) during complete submergence—importance of light and floodwater O<sub>2</sub>. *New Phytol.* 2013;197(4):1193-203.
73. Tadege M, Dupuis I, Kuhlemeier C. Ethanolic fermentation: new functions for an old pathway. *Trends Plant Sci.* 1999;4(8):320-5.
74. Panda D, Sharma SG, Sarkar RK. Chlorophyll fluorescence parameters, CO<sub>2</sub> photosynthetic rate and regeneration capacity as a result of complete submergence and subsequent re-emergence in rice (*Oryza sativa* L.). *Aquat. Bot.* 2008;88(2):127-33.
75. Fukao T, Yeung E, Bailey-Serres J. The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. *Plant Cell.* 2011;23(1):412-27.
76. Panda D, Sarkar RK. Characterization of leaf gas exchange and anti-oxidant defense of rice (*Oryza sativa* L.) cultivars differing in submergence tolerance owing to complete submergence and consequent re-aeration. *Agric. Res.* 2013;2:301-8.
77. Xu K, Mackill DJ. A major locus for submergence tolerance mapped on rice chromosome 9. *Mol. Breed.* 1996;2:219-24.
78. Hattori Y, Nagai K, Furukawa S, Song X-J, Kawano R, Sakakibara H et al. The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. *Nature.* 2009;460(7258):1026-30.

79. Gao X-H, Xiao S-L, Yao Q-F, Wang Y-J, Fu X-D. An updated GA signaling 'relief of repression' regulatory model. *Mol. Plant*. 2011;4(4):601-6.
80. Fukao T, Bailey-Serres J. Submergence tolerance conferred by Sub1A is mediated by SLR1 and SLRL1 restriction of gibberellin responses in rice. *Proc. Natl. Acad. Sci. U.S.A.* 2008;105(43):16814-9.
81. Fukao T, Xu K, Ronald PC, Bailey-Serres J. A variable cluster of ethylene response factor-like genes regulates metabolic and developmental acclimation responses to submergence in rice. *Plant Cell*. 2006;18(8):2021-34.
82. Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S et al. Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. *Nature*. 2006;442(7103):705-8.
83. Neeraja CN, Maghirang-Rodriguez R, Pamplona A, Heuer S, Collard BC, Septiningsih EM et al. A marker-assisted backcross approach for developing submergence-tolerant rice cultivars. *Theor. Appl. Genet.* 2007;115:767-76.
84. Singh S, Mackill DJ, Ismail AM. Physiological basis of tolerance to complete submergence in rice involves genetic factors in addition to the SUB1 gene. *AoB Plants*. 2014;6:plu060.
85. Hussain W, Anumalla M, Ismail AM, Walia H, Singh VK, Kohli A et al. Revisiting FR13A for Submergence Tolerance-Beyond the SUB1A Gene. *J. Exp. Bot.* 2024;erae299.
86. Phukon M, Das J, Sruthi R, Verma RK, Modi MK, Bhattacharyya A et al. Study on submergence tolerance of rice (*Oryza sativa* L.) in a core panel of North-East India using GWAS. *Indian J. Genet. Plant Breed.* 2024;84(02):193-201.
87. Chetia SK, Kalita M, Verma RK, Barua B, Ahmed T, Modi M et al. Flood proofing of Ranjit, a popular variety of North-Eastern India through transfer of Sub1 rice QTL by modified marker-assisted backcross breeding. *Indian J. Genet. Plant Breed.* 2018;78(02):166-73.
88. Pandit E, Pawar S, Barik SR, Mohanty SP, Meher J, Pradhan SK. Marker-assisted backcross breeding for improvement of submergence tolerance and grain yield in the popular rice variety 'Maudamani'. *Agronomy*. 2021;11(7):1263.
89. Dar MH, De Janvry A, Emerick K, Raitzer D, Sadoulet E. Flood-tolerant rice reduces yield variability and raises expected yield, differentially benefitting socially disadvantaged groups. *Sci. Rep.* 2013;3(1):3315.
90. Ravindra R, Singh A, Perumal A. Innovations and investments for transforming India's rice economy: Submergence tolerant rice varieties in rainfed lowlands of North-Eastern Uttar Pradesh. *Indian J. Agric. Sci.* 2020;90(1):3-8.
91. Akintayo O, Daniel I, Afeez S, Jolayemi O, Semwal V, Venuprasad R. qSUB2: A novel QTL with positive epistasis with SUB1 locus enhances submergence tolerance in rice. *Crop Sci.* 2023;63(3):1246-56.
92. Jang S-G, Kim Y, Kwon S-W. Detection of QTLs related to submergence tolerance on germination stage in rice (*Oryza sativa* L.). *Korean J. Breed. Sci.* 2022;54(4):369-74.
93. Kong W, Li S, Zhang C, Qiang Y, Li Y. Combination of quantitative trait locus (QTL) mapping and transcriptome analysis reveals submerged germination QTLs and candidate genes controlling coleoptile length in rice. *Food Energy Secur.* 2022;11(1):e354.
94. Septiningsih EM, Sanchez DL, Singh N, Sendon PM, Pamplona AM, Heuer S et al. Identifying novel QTLs for submergence tolerance in rice cultivars IR72 and Madabaru. *Theor. Appl. Genet.* 2012;124:867-74.
95. Quimio CA, Torrizo LB, Setter TL, Ellis M, Grover A, Abrigo EM et al. Enhancement of submergence tolerance in transgenic rice overproducing pyruvate decarboxylase. *J. Plant Physiol.* 2000;156(4):516-21.
96. Wang S, Liu W, He Y, Adegoke TV, Ying J, Tong X et al. bZIP72 promotes submerged rice seed germination and coleoptile elongation by activating ADH1. *Plant Physiol Bioch.* 2021;169:112-8.
97. Liang S, Xiong W, Yin C, Xie X, Jin Y-j, Zhang S et al. Overexpression of OsARD1 improves submergence, drought, and salt tolerances of seedling through the enhancement of ethylene synthesis in rice. *Front. Plant Sc.* 2019;10:1088.
98. Duan A, Liu R, Liu C, Wu F, Su H, Zhou S et al. Mutation of the gene encoding the PHD-type transcription factor SAB23 confers submergence tolerance in rice. *J. Exp. Bot.* 2024;75(1):168-79.

99. Li X, Peng R-H, Fan H-Q, Xiong A-S, Yao Q-H, Cheng Z-M et al. *Vitreoscilla* hemoglobin overexpression increases submergence tolerance in cabbage. *Plant Cell Rep.* 2005;23:710-5.
100. Taylor-Kearney LJ, Flashman E. Targeting plant cysteine oxidase activity for improved submergence tolerance. *Plant J.* 2022;109(4):779-88.

**Disclaimer/Publisher's Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of the publisher and/or the editor(s). This publisher and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.

© Copyright (2024): Author(s). The licensee is the journal publisher. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

*Peer-review history:*

*The peer review history for this paper can be accessed here:*

<https://www.sdiarticle5.com/review-history/121547>