Review Article

Mechanistic Insights and Genetic Approaches for Enhancing Submergence Tolerance in Rice

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 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: Rice, Submergence Tolerance, Abiotic stress, MAS, Sub1, QTL

1. INTRODUCTION

Rice, which belongs to the poaceae family, is a key 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, 2, 3, 4, 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, 4, 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, 4, 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 awide 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, withabsolutely 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, 23, 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, 26, 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, 34, 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 ($ONOO^-$) 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.

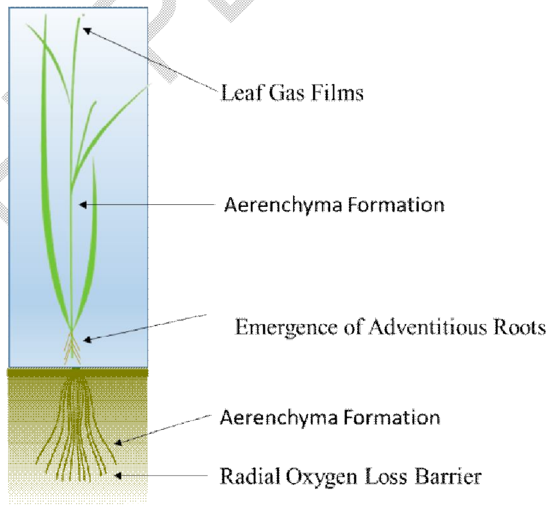

Fig. 1: Anatomical and Morphological Adaptations in Rice to Submergence Condition

3.1.2 EFFECTIVE BARRIERS TO RADIAL OXYGEN LOSS

In roots, oxygen moves longitudinally via the aerenchymaandcan 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_2 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_2S, Fe_2^+, and carboxylic acids, produced by anaerobic bacteria in anoxic soils [39, 40, 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 exodermalsuberization that creates a barrier to radial oxygen loss in rice roots [43].The ROL barrier also restricts gas diffusion, including H_2, water vapor, and H_2S, and apoplastic movements of water, Na^+, and Fe_2^+[39, 44, 45, 46]. This multifunctional trait, combined with the formation of thick adventitious roots under soil flooding, conserves O_2 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, 50, 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, 53, 54, 55]. These gas films play a pivotal role in enhancing photosynthetic rates by facilitating rapid CO_2 diffusion to stomata and allowing O_2 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 theremoval 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, 63, 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_2O_2 production and enhancing ethylene signaling by inhibiting the H_2O_2 scavenger gene *MT2b*[63]. Ethylene also synergizes with gibberellin to induce AR formation, a process repressed by theapplication of exogenous ABA [65]. The absence of O_2 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].

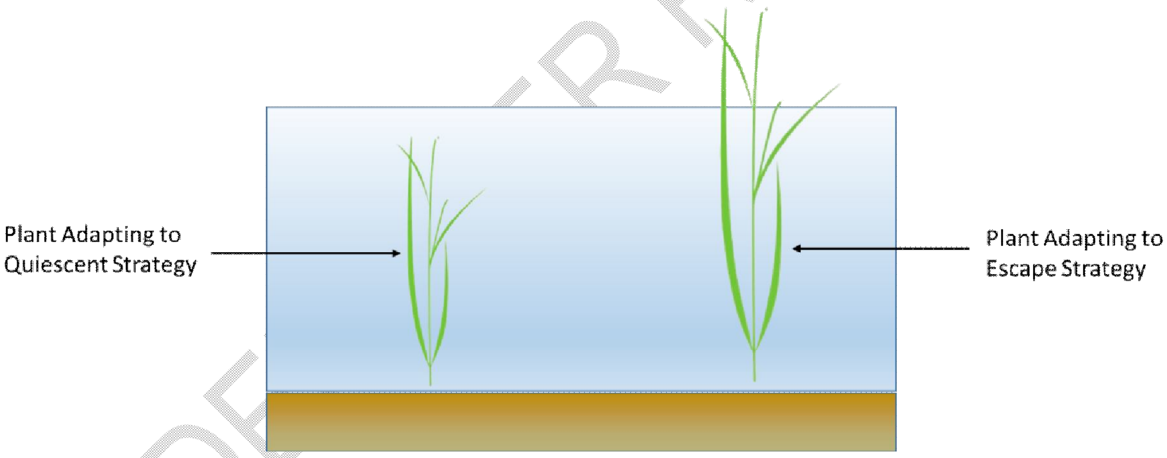

Fig. 2: Rice Response to Submergence Condition through Different Strategies

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].

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, 82, 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].

4.0 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 animportant 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 Thadokkham1 [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$_3$F$_1$ 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$_2$ 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$_2$F$_2$ 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.	*qSUB1*	165 RILs derived from crosses between 'Milyang	9.44%	[92]
3.	*qSUB3*		14.62%	
4.	*qSUB4*		9.74%	

5.	*qSUB7*	23' and 'Tong 88-7'	7.09%	
6.	*qCL-1.1*	272 RILs from crosses between ‘Luohui 9’ and ‘RPY geng’	7.14%	[93]
7.	*qCL-3.1*		8.81%	
8.	qSUB1.1	$F_{2:3}$ population between ‘IR72’ and ‘Madabaru’	52.3%	[94]
9.	qSUB2.1		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+, NADH, and ATP. These metabolites play crucial roles in the alcoholic fermentation and glycolysis pathway, ultimately generating essential energy reserves that confer resistance 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^2 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.

5.0 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.

6.0 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.

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