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REVIEW ARTICLE

Genetics, Physiological Mechanism and Breeding for Tolerance against Submergence, Salinity, and Saline-Submergence Stress in Rice (*Oryza sativa* L.)

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Abstract

Rice is a staple food and one of the most crucial crops globally, providing sustenance for more than half of the world's population. Climate change has a crucial impact on the agricultural sector, particularly rice cultivation, due to the increase in abiotic stress incidences. Salinity is one of the most severe abiotic stresses on rice production globally. Salt stress significantly reduces growth performance, affecting various metabolic and physiological processes in rice. Submergence is another type of abiotic stress affecting rice growth and yield. Recently, a newly emerged abiotic stress called saline submergence may also jeopardize rice production. Seawater intrusion into rice fields located nearby coastal areas may cause saline flash floods, especially during monsoon season. Rice cultivated in coastal areas is prone to saline-submergence stress, leading to a significantly lower yield. Although *Sub1* and *Saltol* QTLs are widely used in developing rice cultivars with submergence and salinity tolerance, there is a lack of studies conducted to explore the potential performance of breeding lines with *Sub1* and *Saltol* QTLs under saline-submergence stress. It has been hypothesized that the introgression of *Sub1* and *Saltol* QTLs into elite rice cultivars might result in potentially tolerant breeding lines to saline-submergence stress. Further breeding projects, however, need to be conducted to prove this postulation. The present mini-review deals with genetics, physiological mechanisms, and breeding achievements for submergence and salinity-tolerant rice while at the same time highlighting saline-submergence as an emerging type of abiotic stress in rice cultivation.

Keywords

Flood; Marker-assisted selection; *Saltol*; *Sub1*; Quantitative trait loci

Introduction

Climate change is becoming a global concern, especially in the agricultural sector, affecting food security. The latest report by the Intergovernmental Panel on Climate Change (IPCC) revealed that climate change has reduced food security, affected water security, increased global temperature, glacier melting, and global sea rice, hampering efforts to meet Sustainable Development Goals (1). Indeed, global warming is causing glaciers and ice sheets around the planet to melt leading to the raising of sea levels (2). This is corroborated by the latest report by IPCC which predicts that global temperature was to be 1.1° C warmer in the years 2011-2020 as compared to 1850-1900 (1).

As a result of global warming and glaciers melting, the frequency of floods increases leading to submergence stress on rice fields, particularly in the rainfed lowlands of the South and Southeast Asia region (3). Taking Malaysia as an example, the rainfall record for 40 years, from 1978 until 2017, indicated an uptrend in the average annual rainfall every decade, with the East Coast of Malaysia receiving a high amount of rainfall during the northeast monsoon season (4). The previous report indicated that about 40,828.28 hectares of rice fields in Malaysia were destroyed by flood with a total loss of 128.80 million ringgits, referring to data recorded between 2017 and 2021 by the Ministry of Agriculture and Food Industry (MAFI), Malaysia (4). On a global view, it was projected that the rice bowl of the world mainly in the Indian subcontinent and parts of China might experience increased precipitation and flooding by the year 2030 (5). Kurniasih *et al.* (6) also reported that rice production in Indonesia was affected by climate change such as flooding and salinity.

In addition, coastal erosion is recently becoming one of the rising problems (7). Azid *et al.* (8) defined coastal erosion as the physical wearing of surface materials by currents, wave action, and tidal currents. Heavy storms would create high tides and strong waves, damaging the beach and reducing the sea bank (9). Once the sea bank is degraded, the seawater may overflow into low-lying areas, leading to saline water flooding (10). According to Kumar *et al.* (11), saline water is projected to penetrate further inland, drastically altering the topography of the deltas and coastal plains by the year 2050, affecting around 50 percent of global arable lands. Rice, however, is susceptible to abiotic stresses such as drought, flood, salinity, and saline submergence among others (12,13). For instance, once the salty water gets into the rice field, salt may ruin the land when the flood subsides. Prolonged exposure to saline water floods might cause adverse effects on soil and rice productivity (9). Seawater intrusion into rice fields near coastal areas during the monsoon season may create a new type of abiotic stress known as saline submergence (10). This mini-review will emphasize the genetics, physiological mechanism, and breeding achievement for submergence and salinity-tolerant rice whilst simultaneously highlighting saline submergence as an emerging type of abiotic stress in rice cultivation.

Methodology

In finding the related articles and journals, several academic database platforms were used such as Scopus (https://www.scopus.com/search/form.uri?display=basic), Google Scholar (https://scholar.google.com/), and Science Direct (https://www.sciencedirect.com/). The process started with the identification of related terms derived from the manuscript title. The list of search terms used for this review was rice breeding, rice and salinity, saline water and submergence in rice, *Saltol*, rice and submergence, *Sub1,* and rice abiotic stress. For this manuscript, there is no specific inclusion of the publications searched while the publications before 2005 were excluded unless for an important rice submergence tolerance manuscript published in 1996. The process continued with the classification of the journals and articles into specific objectives. Then, the summarization of the journals and articles was performed before the write-up of the review article started. Finally, Canva online software and Microsoft PowerPoint from Microsoft 365 were used for figure production.

Effects of Submergence Stress on Rice

In Southeast Asia, flash floods might be the most common flood during the monsoon season (10). Such an event may cause submergence stress to newly planted rice. Iftekharuddaula *et al.* (14) stated that plants' survival during submergence depended on the depth, duration, and water quality vis-à-vis the flood water's salinity level. Septiningsih *et al.* (15) reiterated that the survival rate of rice under complete submergence will depend on environmental conditions such as temperature, water turbidity, solar radiation, and soil fertility. Nonetheless, Oladosu *et al.* (16) mentioned that rice might escape submergence stress by lengthening its internode under complete submergence conditions. However, the affected plant tends to be lodged after the flood and eventually dies due to carbohydrate shortage, limited nutrient supply, and disrupted biochemical processes (9).

Nonetheless, other parts of Asia may suffer a prolonged flood ranging between two weeks or more with the flood water remaining in the rice field causing prolonged submergence of rice (17) The affected rice will generally end with poor tillering leading to low-yield production. According to Oladosu *et al.* (16), the affected submerged plants recorded a lower panicle number, number of grains per panicle, grain-filling percentage, and delays in flowering and maturity, causing a reduction in yield production. During submergence, limited light interception and absorption significantly reduced the photosynthetic rate of the plant (18). In addition, restricted gas diffusion due to stomatal closure would affect rice metabolism, biochemical processes, and survival under prolonged submergence with the older leaves incurred damage, and no new leaves emerged (19) Complete submergence also induces the production of reactive oxygen species (ROS) such as hydrogen peroxide, hydroxyl radical, and superoxide anion that, if not moderated, would disrupt normal cellular processes such as mitosis and meiosis leading to plant death (16).

Effects of Salinity Stress on Rice

Rice is categorized as a salt-sensitive plant and the yield of rice in a saline environment was substantially less than in a non-saline environment (20). Salinity could be regarded as a second to drought as significant stress decreasing rice production worldwide (21). Rice has a salt stress threshold of about 4 dS/m, and every dS/m beyond this results in a 12% yield decrease, making rice a salt-sensitive crop (22). Rice's salt susceptibility varies based on its developmental phase. Rice is much more tolerant to salinity during germination than in later phases of development (21). It becomes sensitive during the seedling stage, recovers a degree of resistance during vegetative growth, and becomes highly vulnerable during the reproductive stage (21). Salinity influences panicle length and spikelet quantity per panicle, delaying panicle emergence, flowering, and rice grain production (23). Furthermore, as pollen viability is reduced, salinity will affect the proportion of egg cells fertilized and, consequently, rice yield (24).

In addition, an excessive Na+ and Cl– ion in rice leaves damage the chlorophyll concentration, inhibiting PSII primary electron transport (25). Increased salt levels restrict plant development by reducing CO_2 absorption, resulting in stomatal closure and a lower intracellular CO_2 partial pressure, which leads to a lower photosynthetic rate (26). During salt stress, the build-up of intracellular sodium ions alters the Na^+/K^+ ratio, affecting photosynthetic bioenergetic systems (25). According to Pattanagul and Thitisaksakul (27), the salinity will cause plants to suffer from osmotic inhibition and ionic toxicity. The osmotic inhibition and ionic toxicity occurred when there was a high salt concentration in water. Besides that, the excessive salt in the soil will allow plants to lose more water by transpiration, thus, the excess Na^+ ion in the ground will be absorbed by the plant and eventually cause osmotic stress to the cell (25).

Effects of Saline-Submergence Stress on Rice

As compared to submergence and salinity stresses, the effects of saline water submergence stress on rice are still poorly documented (Table 1). However, as shown in Fig. 1., rice plants that were immersed in salt water may experience ionic and osmotic stress (i.e., high Na^+ and Cl^- concentration, low K+ concentration, imbalance Na^+/K^+ ratio, etc.) due to salinity, in addition to oxidative stress (i.e., limited light interception, gas diffusion, rate of photosynthesis, etc.) due to complete submergence. As reported by Sazali *et al.* (10) seedling growth attributes of rice were significantly affected under saline-submergence at 4, 8, and 12 dS/m. The study was carried out using selected rice cultivars from Malaysia mainly MR297, MR284, and MR253, along with a universal salinity tolerant check, Pokkali, and submergence tolerant check, IR64-Sub1. The IR64-*Sub1* recorded a significantly higher survival rate at 83% under freshwater submergence (0 dS/m) as compared to other genotypes. However, both tolerant checks, IR64-*Sub1* and Pokkali along with other genotypes were not survived under saline-submergence at 4, 8, and 12 dS/m indicating susceptibility to saline-submergence stress (10). In the future, additional research could be performed to comprehend the impact of saline water submergence on rice growth and development.

Genetics, Physiological Mechanism and Breeding for Submergence Tolerant Rice

During the 1970s, the International Rice Research Institution (IRRI) launched systematic research to identify submergence-tolerant germplasm with thousands of accessions from the international germplasm collection screened under complete submergence in a water tank (28). The screening revealed two germplasm, FR13A, and FR43B, originated from Odisha, Eastern India, with remarkable submergence tolerance (28). Xu and Mackill (29) also reported a sizable QTL for submergence tolerance in rice (known as *Sub1*) on chromosome 9 using the Random Amplified Polymorphic (RAPD) and Restriction Fragment Length Polymorphism (RFLP) markers from FR13A. In the F_2–F_3 population, *Sub1* was found to be responsible for almost 70% of the phenotypic variance for a higher survival rate under complete submergence for 14 consecutive days (29). *Sub1* was later fine-mapped to a sufficiently narrow gap of chromosome 9 from RZ698 to C1232 to allow marker-assisted selection (MAS) using tightly linked markers (29). Three *Sub1* clusters were then

Table 1. Rice response to submergence, salinity, and saline water submergence stress

Abiotic Stress	Key Response	Trait	Tolerance	Reference
Submergence	Oxidative and respiration stress with limited gaseous exchange	Survival rate, shoot elongation, leaf gas exchange, starch, sugar and chlorophyll content, grain yield, plant height, dry mass, number of tillers, and ethylene concentration	Quiescence	(14), (52) (26), (53)
	Poor growth performance	Plant height, number of tillers	Escape	(16)
Salinity	Low ionic homeostasis and delayed flowering	Plant height, biomass, number of panicles, panicle length, days to flowering, Na+ and K+ concentration, grain yield, and	-	(54)
	Low rate of photosynthesis	Photosynthesis and transpiration rate, intercellular CO_2 concentration, stomatal conductance, and number of filled grains	-	(55) (56)
	Poor growth and agronomic performance	Plant height, survival rate, days to 50% flowering, total biomass, number of effective tillers per plant, panicle length, spikelet fertility, grain yield, and Na+/K+ ratio	-	(42) (57), (58)
Saline water submergence	Poor growth performance	Plant height, and survival rate	Quiescence and escape mechanism	(10)
	Poor seed germination	Plant height, number of leaves, chlorophyll content, root length, and plant biomass	-	(6)

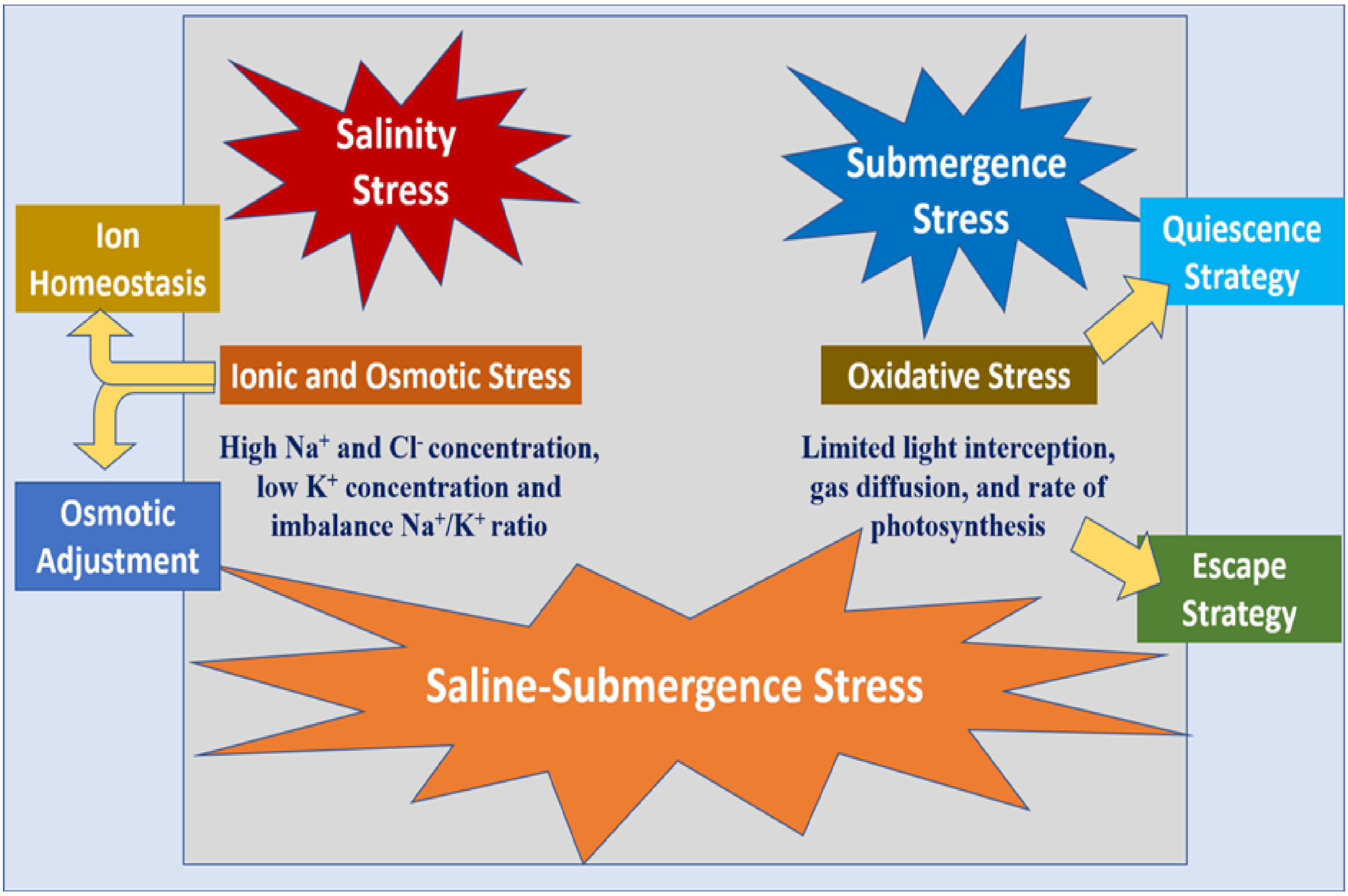

Fig. 1. Hypothetical effects of saline-submergence stress and tolerance strategies

identified as *Sub1A*, *Sub1B,* and *Sub1C* (3). Among those three clusters, *Sub1A* was the most significant due to its major role in tolerance against submergence stress (3). The FR31A was widely used as a donor parent in breeding for submergence tolerance, QTL association mapping, and cloning of the *Sub1* gene (16).

In general, *Sub1* would be up-regulated during exposure to complete submergence and subsequently down-regulated once the flood subsides. *Sub1* is associated with an Ethylene Responsive Factor (ERF) like mechanism, a plant protein widely known as a regulator for abiotic and biotic stress responses (3). A previous study on ERFs found that *Sub1A* was responsible for submergence tolerance (30,31). The *Sub1A* locus identified two important alleles called *Sub1A*-1 as the tolerant allele and *Sub1A*-2 as the intolerant allele (30,31). *Sub1A*-1 allele has been a major determinant of submergence as the gene was present in the *Sub1* donor variety, FR13A (29). *Sub1A*-1 tolerant mechanism works by applying the quiescence strategy where the elongation of shoots was suppressed during submergence stress (32). The quiescence strategy allows the plant to preserve the energy for survival during complete submergence and after the flood subsides. Submergence tolerant genotype with the *Sub1A*-1 allele recorded a shorter plant height under submergence stress than the susceptible genotype (30,31). Apart from the quiescence strategy, plants under complete submergence may activate the escape strategy (32). In the process of escaping complete submergence, plants with an escape strategy would elongate their shoot thus consequently having higher plant height (16). Moreover, plants with an escape strategy secret ethylene which leads to an increment of gibberellic acid (GA) production, a hormone that is responsible for shoot elongation (32). Hence, the plant tends to elongate its shoot to escape submergence stress. However, the elongated plants might suffer from lodging stress after the flood subsided, making the escape strategy less effective than the quiescence strategy (16).

Breeding for submergence-tolerant rice was started simultaneously with identifying the *Sub1A*-1 allele in FR13A with the FR13A-derived breeding line IR49830-7-1-2-2 having *Sub1A*-1 allele and other favourable agronomic traits was successfully developed in the mid-1990s (28). Since then, efforts have been made to introgressed *Sub1A*-1 alleles into rice mega- and elite-cultivars such as Samba Mahsuri, Swarna, and IR64 (33, 34). As an outcome, near-isogenic lines (NILs) of those cultivars with *Sub1A* and good agronomic traits were successfully generated and released for commercial cultivation as Samba Mahsuri-*Sub1*, Swarna-*Sub1*, and IR64-*Sub1* (34). Those NILs were developed using marker-assisted backcrossing (MABC) strategy with an FR13A-derived breeding line as a tolerant donor and Samba Mahsuri, Swarna, and IR64 as recurrent parents (33, 34). Later, a MABC procedure was developed to introduce *Sub1* into any rice mega variety (35). The introgression of *Sub1* into any cultivar could be achieved within a 2-3 year timeframe, using a tightly linked cleaved amplified polymorphic sequence (CAPS) marker such as GNS2, and a microsatellite marker like AEX1 (35). Other than MABC, an advanced method such as genotyping by sequencing (GBS) may also be used to speed up the breeding process (14). Another promising avenue is the development of high-yielding hybrid rice cultivars with submergence-tolerant *Sub1A* to improve yield potential in flood-prone areas.

Genetics, Physiological Mechanism and Breeding for Salinity Tolerant Rice

According to Waziri *et al.* (36), Pokkali is a traditional cultivar that is naturally resistant to salt stress due to generations of adaptation to thrive on salt-affected soil, making it a high-potential salt-tolerant donor. A major QTL, called *Saltol* contributed to this desirable adaptation (36). *Saltol* was discovered on chromosome 1 in an F_8 recombinant inbred lines (RILs) of the Pokkali (salt tolerant) x IR29 (salt-sensitive) population developed at IRRI in their salt stress tolerance breeding program (37). A set of 78 putative RILs was generated and employed to map *Saltol* through the utilization of amplified fragment length polymorphism (AFLP) markers (37). The *Saltol* region was then fine-mapped in between 10.7-12.2 Mb of chromosome 1 using RFLP and microsatellite markers in a population of 54 RILs (38). In addition, RILs FL478 was found to have a region in between 10.6-11.5 Mb of chromosome 1 originating from Pokkali and was flanked by IR29 alleles (39). The subsequent studies managed to re -map several QTLs for salinity tolerance on different chromosomes in rice (36). Moreover, the expression of *Saltol* was to be localized between 10.8-16.4 Mb in chromosome 1 (40). According to Waziri *et al.* (36), about 783 loci were detected within *Saltol,* which encoded unknown proteins suggesting that salinity tolerance in rice is polygenic with various genes activating different tolerant metabolism.

In general, *Saltol* was associated with the Na^+/K^+ ratio and seedling stage salinity tolerance (41). It was found to be responsible for low Na+ absorption, high K^+ absorption, and a low Na^+-to-K^+ ratio in salinity-stressed rice shoots (42). The increase in K^+ absorption will inhibit Na^+ uptake, hence, the toxicity effect of Na^+ could be reduced (42). Previously, Bonilla *et al.* (38) reported that 43% of the phenotypic variation for shoot Na^+/K^+ ratio in a population of 54 RILs Pokkali x IR29 was associated with *Saltol*. A subsequent study by Thomson *et al.* (41) confirmed that *Saltol* contributes to Na^+/K^+ homeostasis and 64.3-80.2% variation of Na^+/K^+ ratio at rice shoot. Moreover, Singh *et al.* (43) found that the Na^+/K^+ homeostasis mechanism was activated under salinity stress during an introgression of *Saltol* into Pusa Basmati 1 via MAS. They also observed the movement of Na^+ and K^+ through intrusive apoplastic transport in the salinity-susceptible lines where cation was highly accumulated in the shoot compared with the root (43). They then concluded that *Saltol* contributes to salinity tolerance by restricting the accumulation of Na^+ in the shoot, suggesting that Na^+ plays a significant role in regulating salinity tolerance in rice (43).

Massive genetic resources have provided information to develop molecular markers of specific target gene(s) or QTL(s) regarding improving varieties with desirable traits. In this way, the breeding program could be accelerated as the screening phase could be shortened. Through MAS, a faster selection and identification of *Saltol* introgressed lines has been achieved. The discovery of the *Saltol* region in RILs FL478 accelerated rice breeding for salinity tolerance (41). Since then, many countries such as India, Bangladesh, Philippines, Thailand, South Korea, Japan, and the United States have been developing salt-tolerance rice by introgressing *Saltol* into their elite rice cultivars (44). For instance, *Saltol* was successfully introgressed into popular rice cultivars such as Pusa Basmati, BRRI dhan 28, IR64, BR11, and Swarna via MAS using three SSR tightly linked markers mainly RM8094, RM3412, and RM493 for foreground selection (45).

Saline-Submergence as an Emerging Type of Abiotic Stress in Rice Cultivation

Climate change contributed to about 11–16 cm rise in global mean sea level (MSL) in the twentieth century (46). An increase in MSL will push high tide lines around the earth, covering a significant portion of the current land area causing nations such as China, India, Vietnam, Thailand, and others to likely experience annual coastal flooding problems by 2050 (47). Rice cultivation in coastal areas is also affected due to increased cyclonic storm frequency and seawater intrusion further inland (48). Indeed, rice yield in coastal areas is declining due to seawater intrusion (9).

On the other notes, as far as rice breeding is concerned, although there were several studies conducted in an attempt to combine *Saltol* and *Sub1* QTLs into a single plant using the MAS approach, those studies focused on producing new rice variety with the tolerant ability to salinity and submergence stresses, but not specifically for saline water submergence stress (Fig. 2.). For instance, Das *et al.* (49) successfully pyramided 10 QTLs and genes, mainly bacterial blight-resistant genes (i.e. *Xa4, Xa5, Xa13,* and *Xa21*), the blast-resistant genes (i.e. *Pi2,* and *Pi9*), the gall midge resistance genes (i.e. *Gm1,* and *Gm4*), the submergence tolerant (i.e. *Sub1*) and salinity tolerant (i.e. *Saltol*) into Tapaswini variety to develop an elite cultivar with broader biotic and abiotic tolerance/resistance. Muthu *et al.* (50) on the other hand, pyramided three QTLs vis-à-vis *Sub1*, *Saltol,* and drought grain yield QTL (*qDTYs*) into a popular South India rice variety, Improved White Ponni (IWP). More recently, Nair and Shylaraj (51) introgressed *Sub1* and *Saltol* QTLs into Aiswarya, a mega rice cultivar in South Asia. However, the developed breeding lines were tested under salinity and submergence but not under saline-submergence stress. Hence, further breeding projects could be conducted to determine the performance of rice pyramided lines with both *Sub1* and *Saltol* QTLs under a saline-submergence environment, as shown in Fig. 2.

Conclusion

This review highlighted the genetics, physiological mechanisms, and breeding achievements for submergence and salinity tolerance in rice while opening up a new avenue for saline-submergence as an emerging type of abiotic stress in rice cultivation. Currently, there is a lack of studies exploring the genetics and physiological mechanism of rice under saline-submergence stress. Pyramiding *Sub1* and *Saltol* QTLs into an elite rice cultivar

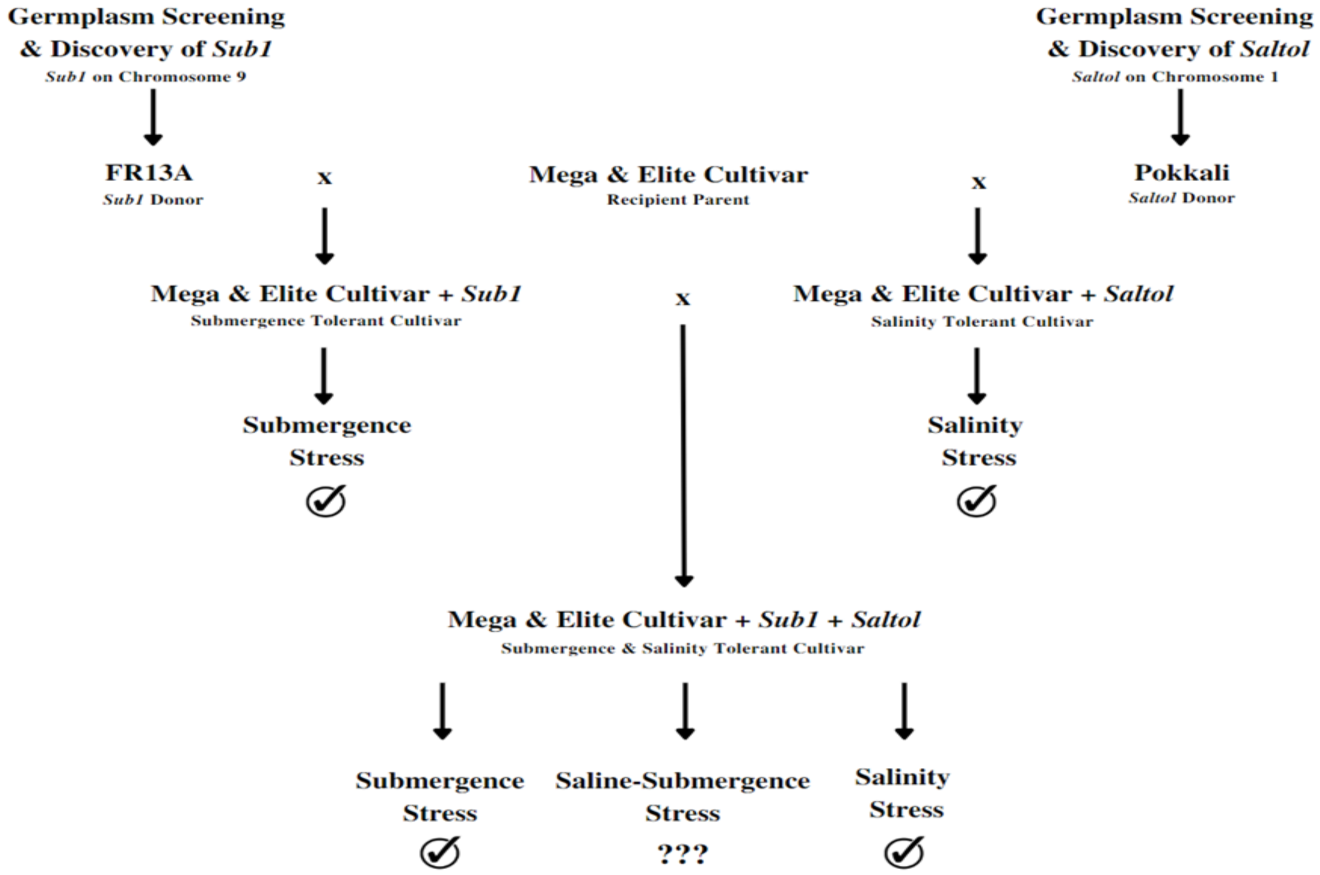

Fig. 2. Marker-assisted Pyramiding of *Sub1* and *Saltol* QTLs into Mega and Elite Cultivar

might result in tolerant breeding lines against saline submergence. Further breeding projects, however, need to be conducted to prove this postulation. Germplasm screening to identify genotypes tolerant to saline-submergence stress may also be conducted. The identified tolerant germplasm could be later used as a donor in a breeding project for saline-submergence tolerant rice.

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Authors' contributions

All authors have contributed equally to composing the manuscript and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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