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REVIEW ARTICLE

Recent Advances of Genetic Resources, Genes and Genetic Approaches for Flooding Tolerance in Rice

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Abstract: Flooding is one of the most hazardous natural disasters and a major stress constraint to rice production throughout the world, which results in huge economic losses. The frequency and duration of flooding is predicted to increase in near future as a result of global climate change. Breeding of flooding tolerance in rice is a challenging task because of the complexity of the component traits, screening technique, environmental factors and genetic interactions. A great progress has been made during last two decades to find out the flooding tolerance mechanism in rice. An important breakthrough in submergence research was achieved by the identification of major quantitative trait locus (QTL) *SUB1* in rice chromosomes that acts as the primary contributor for tolerance. This enabled the use of marker-assisted backcrossing (MABC) to transfer *SUB1* QTL into popular varieties which showed yield advantages in flood prone areas. However, *SUB1* varieties are not always tolerant to stagnant flooding and flooding during germination stage. So, gene pyramiding approach can be used by combining several important traits to develop new breeding rice lines that confer tolerances to different types of flooding. This review highlights the important germplasm/genetic resources of rice to different types of flooding stress. A brief discussion on the genes and genetic mechanism in rice exhibited to different types of flooding tolerance was discussed for the development of flood tolerant rice variety. Further research on developing multiple stresses tolerant rice can be achieved by combining *SUB1* with other tolerance traits/genes for wider adaptation in the rain-fed rice ecosystems.

Keywords: Anaerobic germination potential, marker-assisted backcrossing, stagnant flooding, submergence, *SUB1*, rice.

1. INTRODUCTION

Flooding is one of the main threats to agricultural productivity, affecting the global food supply and food security. In recent decades, the global flood risk has increased dramatically as a result of rapid change in global climate [1, 2]. The intensity and frequency of flooding events are more likely to be recurring due to future climate change scenarios [3-8]. Rice (*Oryza sativa* L.) is an important crop globally, feeding more than 3.5 billion people globally and approximately 90% of rice is grown and consumed only in Asia [9-11]. Unlike other cereals, rice is adapted to the aquatic environment, but severe flooding has a detrimental effect on plant growth, development and in its production [12, 13]. The unpredictable occurrence of this catastrophic flooding results in tremendous annual yield losses in rice [1, 14]. It is being predicted that high rainfall storms will substantially affect rice-growing areas in the near future [4, 15, 16]. Currently, more than 35% of rice fields around the world are subjected to flooding/submergence; leading to food insecurity, predominantly in Asia and Africa [17]. Among South and Southeast Asian countries, the largest area under rainfed lowland and flood-prone ecosystem is occupied by India so far. The flood-affected area in India has escalated to 40 million hectares from 19 million hectares just in a decade's span [18], which posed a great threat to crop productivity and farm income in these areas. Significant progress was made in flooding tolerance research was the identification of major quantitative trait locus (QTL) *SUB1* in rice chromosomes, which is the primary contributor for tolerance. Apart from that, several other QTLs such as *AG1*, *AG2*, *SK1* and *SK2,etc.* identified in different chromosomes available for molecular marker technology to develop flood-tolerant varieties through marker-assisted backcrossing (MABC) strategy. However, the available flash flood-tolerant genotypes cannot withstand stagnant flooding for longer duration or flooding during germination. So, it is necessary to develop more tolerant genotype which can withstand more severe and prolonged submergence stress. Significant progress has been accomplished for developing flooding tolerant rice varieties, to counteract the adverse impact of flooding stress through conventional and molecular breeding approach [19]. However, to combat the anticipated water extremes in future, these efforts should be continued for further improvement of rice breeding under different types of flooding stress [20]. Therefore, there is an immediate need to develop high

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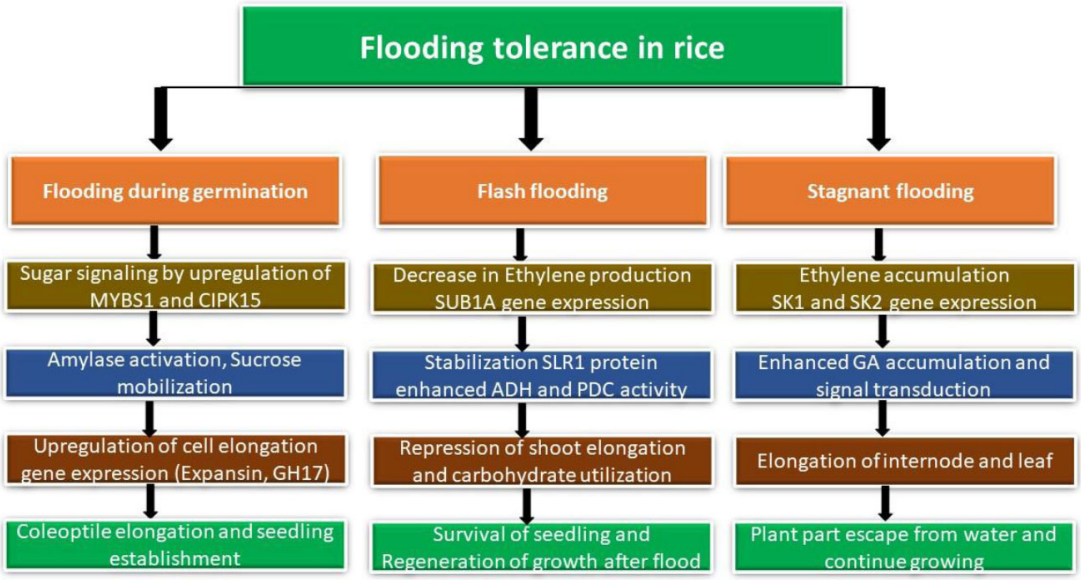

Fig. (1). Molecular mechanism of different types of flooding tolerance in rice. MYBS1: Myeloblastosis sugar response complex 1; CIPK15: calcineurin B-like interacting protein kinase 15; *SUB1A: Submergence 1A*; SLR1: slender rice-1; ADH: alcohol dehydrogenase; PDC: pyruvate decarboxylase; *SK: Snorkel*; GA: gibberellic acid. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

yielding cultivars having resistance to various types of flooding stresses which can enhance yield potential in rainfed lands. Greater efforts are required to identify sources of new genes and understand the detailed basis of the molecular mechanism underlying flooding stress tolerance. The review discusses the recent updates on the screening of rice genotypes under different types of flooding stress and to provide an overview on the genetic resources for tolerance to flooding. A brief discussion on the genes and QTLs in rice chromosomes that confer tolerance to different types of flooding was focused for the development of flood tolerant rice variety. Here, we briefly summarise the progress made in applying genomics tools to unravel the molecular and physiological basis for developing flooding tolerant mega rice varieties suitable for rainfed rice ecosystem.

2. TYPES OF FLOODING AND THEIR TOLERANCE RESPONSES

Flooding is basically categorised into three different categories; which include 1) flooding during germination or anaerobic germination; 2) flash flooding/ complete submergence, which occurs for a short duration and 3) long-duration stagnant flooding (both medium depth (25-50 cm) and deep water (50-100 cm)) or floating rice (more than 100 cm). The tolerance strategy of rice plants underlying each type of flooding condition differs greatly with the genotypes and different growth stages. The molecular mechanism underlying different types of flooding and their tolerance responses are presented in Fig. (**1**).

2.1. Flooding During Germination

Rice seeds could germinate under anaerobiosis up to some extent, but it fails to establish under flooded soil after germination. Anaerobic germination (AG) marks the potential of the seed to germinate under oxygen deficient condition, drawing the energy by undergoing anaerobic respiration process [21]. The seeds with high anaerobic germination potential are essential at the initial stages in the cases of 'direct-seeded rice' (DSR) sown in rainfed and flood prone areas [21, 22]. Despite being well adapted to diverse flooding conditions, many rice varieties are extremely susceptible to anaerobic conditions during germination and early growth of embryo [23-28]. The coleoptile extension plays an important role in helping the seedlings to come in contact with the air for the purpose crop establishment. The root development takes place the moments the leaves protrudes upward and get in contact with air [25, 29-32]. However, the tolerant responses are faster coleoptiles elongation, rapid germination rate, expressing 'expansin genes', elevating amylase activity, anaerobic respiration, *etc*. [33-37]. Tolerant-genotypes have the ability of hydrolyzation of starch to metabolize sugars for generating energy through successive glycolysis and alcoholic fermentation [38, 39]. Nowadays, farmers are adapting DSR cultivation due to its operational simplicity, low input demand and other additional advantages over transplanting method [11, 23, 40-43]. However, poor germination, uneven stand establishment, and high weed infestation remain a major constraint that restricts the wide adaptation of DSR cultivation to flood prone areas [41-43]. This is due to the sensitivity of most of the rice varieties to anaerobic conditions at the time of germination. Thus, rice culti-

vars with better anaerobic germination potential at the initial period of growth are highly needed in order to make direct seeding sustainable in both rainfed and irrigated areas [23, 33, 34, 37, 43-45].

2.2. Flash Flooding or Complete Submergence

The most common and perilous type of flooding during the vegetative stage of rice is 'short-term complete inundation', in which flood is transient but completely submerged the plant for one-two weeks [2, 46-48]. This is commonly referred to as 'flash flooding' and generally occurs in rainfed lowland areas as well as flood-prone areas throughout the world. This type of flooding can take place more than once in the growing season and at any time [14]. Statistics revealed that the flash flooding affects the rice cultivation in South and Southeast Asia to the extent of more than 22 million hectares, out of which 6.2 million hectares of land are in India, resulting in significant loss of crop each year [49-54]. Most of the rice genotypes cannot tolerate complete submergence and severely damaged if completely submerged for more than 3 days due to turbidity of flood water [55-59]. The adverse impact of flooding on rice is mainly due to poor underwater gas exchange, which prevents normal biochemical activities like aerobic respiration and photosynthesis [60-63]. Limited gas diffusion is a major problem during flooding [64] because underwater gas diffusion is approximately 10,000 times slower than in air [65, 66]. The adaptive mechanism of tolerant rice varieties to survive under complete submergence involves maintenance of high carbohydrate content before, during and after submergence, slow shoot elongation, better underwater photosynthesis through the retention of chlorophyll content, aerenchyma formation, formation of leaf gas films, regulation of reactive antioxidant species, higher activity of antioxidant systems, quicker regeneration growth after submergence, restriction of ethylene production, *etc* [1, 14, 54, 62, 67-76]. The unique growth control strategy used by tolerant genotypes to complete submergence is 'quiescence strategy (low-oxygen quiescence syndrome). The plant has the capacity to control its growth of root and shoot, preserving the required energy for survival during submergence as well as to resume growth during de-submergence [12, 56, 63, 74, 77, 78]. This strategy is an outcome of insensitivity to ethylene, which suppresses the action of gibberellic acid to check shoot elongation under submergence [79].

2.3. Stagnant Flooding

Stagnant flooding has been a major problem for rice production and is noticed in the low land areas, where the water remains in the fields all through the growing season but gets dries up before harvesting time [52, 80-82]. The water depth ranges from 20 to 50 cm and the water stagnation lasts for a longer duration of about a few weeks to several months [1, 81, 83]. Under stagnant flooding stress, unlike complete submergence, at least 5% of the plants always remain over and above the water surface. The rice plants under stagnant flooding conditions suffer substantial yield losses and the average productivity may vary extensively, ranging from 0.5 to 1.5 t/hm^2 with variance of depth of water [84-86]. Slow elongation growth along with survival under submergence is the main requisite for the stagnant flooding tolerance [87]. Vergara *et al.* [83] also reported that moderate elongation, high tillering ability, limited depletion of carbohydrate reserve and higher fertility support the survival and yield under stagnant flooding condition. So far, very limited attention has been given to stagnant flooding tolerance as compared to other types of flooding stress [83-85, 88]. Therefore, greater efforts are required for the identification of new sources of genetic resources tolerant to stagnant flooding as well as to find out the physio-molecular mechanism of the plant undergoing the stress.

In deep water flooding, water accumulates for a longer period and the floodwater level varies from half a meter to 4 meters. Deepwater rice adapted to submerged conditions by rapid elongation of internodes and leaves to outgrow the flood water in a short period, which helps for efficient photosynthesis and gas exchange [60, 89]. This strategy is an 'escape strategy (low-oxygen escape syndrome)' which triggers faster internode elongation [60]. Normally deepwater flooding is not restricted to one month but continuesfor several months due to landscape situations [1]. Deepwater flooding sometimes involves 'flooding more than 1 meter'. The rice grown in such an area is known as floating rice and with the rising floodwater the plant grows and can gain the height of 25 cm per day [56, 80, 90, 91] and can reach a maximum height of 5 meter to avoid complete submergence. Thereby it succeeds in keeping its leaves and panicles above the surface of the water [92]. The two genes (*SNORKEL1* and *SNORKEL 2*) were cloned, which promote internode elongation by enhancing the biosynthesis of gibberellic acid under deep water flooding conditions [17, 38, 90, 93-95].

3. Screening of Rice Genetic Resources for Flooding Tolerance

The landraces and traditional rice varieties are valuable components to future crop improvement programs as they possess important adaptive traits required to survive in a wide range of stressful environments [96]. Farmers adopt different kinds of traditional rice varieties in vogue under such flood prone areas even though they are low yielding. These rice landraces are exposed to extreme water variability and they become the source of genetic variation for increasing the flooding tolerance in rice through breeding programs [46]. A list of flooding tolerant rice genetic resources identified through screening under different kinds of flooding are presented in Table **1**.

3.1. Genetic Resources for Flooding Tolerance During Germination

The anaerobic germination potential differs significantly in different rice genotypes. It enables some cultivars to grow better than others under flooding during germination [21]. Yamauchi *et al.* [27] identified 12 rice genotypes having higher anaerobic germination potential after screening a total of 662 rice accessions from the gene bank of IRRI

Table 1. List of rice genetic resources identified for tolerance to different types of flooding.

Types of Flooding	Genetic Resources	References
Flooding during germination	Khao Hlan On (KHO), Ma- Zhan Red, Kalongchi, Dholamon 64-3, Khaiyan, Cody, Sossoka, IR68552-100-1-2-2-2, Kaolack, Kharsu, Liu-Tiao-Nuo, Nanhi	[23, 25, 43]
	Kalarata	[129]
	Photo-blastic Rice (PBR)	[131, 187]
	Banajira, Nipponbare	[188, 189]
	Panikekoa, T 1471	[76]
	Basantichudi, Bausaganthi, Patadhan	[33]
	MTU 1140, MTU 2716, SM-2, RTCNP 28, RTCNP 29	[101]
Flash flooding/ Complete submergence	FR13A	[49, 52, 102, 190]
	FR43B, Thavalu, Kurkaruppan, Goda Heenati	[1, 102]
	IR49830-7-1-2-2, BKNFR76106-16-0-1-0, DH206 (IR67819F2-CA-61)	[139, 190, 191]
	Atiranga, CR 2003-13, CR 2006-7, TTB 238-3-38-3 (Prafulla), NDR 8002, CR 2003-2, CR 2003-3, CR 978-8-2, IR40931-26-3-3-5, IR49830-7-1-2-1, AC1303B, INGR04001, INGR08110, AC38575, AC37887, IC258990, IC258830, AC42087, AC20431, INGR08113, INGR08109, AC42091	[76, 108]
	Bhasakalmi, Keralasundari, Meghi	[106]
	Kalojoma, Damsi, DSL-78-8, DG1-349, Putidepa	[110]
	Samudrabali, Basnamundi, Gadaba, Surudaka, Dokarakuji	[46]
Stagnant flooding	IRRI 154 (NSIC Rc222), IRRI 119, IR10F365	[34, 81, 142]
	AC39416A, AC85, AC34280, Sabita, AC736, AC443	[84]
	AC1781, AC1996, AC813, AC85, AC39416A, AC443, AC34280, JRS196, Sabita, IC461224, IC459733, Varshadhan; Utkalprabha, CR1014, Gayatri, Kalashree, Panidhan, Tulasi, Sarala, Hanseswari, CR Dhan 500, CR Dhan 501, CR Dhan 505, Jayanthidhan, Jalmani	[117]
Deep water flooding	Jalmagna, Rayada 16-3, Baisbish	[114, 190]
	Sudu Gries, Nang Dum To	[90, 156]
	C9285	[164]
	Goai, Habiganj, Aman VIII, Badal106; RD19 (Thailand); Hangseswari, Saraswati, Ambika, Sabita; Prachinburi2(Thailand)	[80, 155, 190, 192]
Both Flash flooding and stagnant flooding	INGR08109, INGR08111, NGR08113, AC42091	[87]
	Khao Tah Haeng 17, Leung Pratew 123	[80]

(International Rice Research Institute) and INGER (International Network for the Genetic Evaluation of Rice). Jiang *et al.* [97] also studied 359 rice accessions under 20 cm of water depth, only by assessing variation in coleoptile length. At the initial large-scale screening of more than 8000 rice genotypes at IRRI, only few of them (0.23%) were identified as tolerant to GSOD [23, 25]. This percentage (0.23%) of lines again reduced to 0.06%, following successive evaluation in replicated trials [24]. The six rice genotypes which were identified as tolerant after repeated experiments by Angaji *et al.* [23] include 1. Nanhi (India), 2. Khao Hlan On (Myanmar), 3. Khaiyan (Bangladesh), 4. Kalonchi (Bangladesh), 5. Cody (USA), 6. Ma-Zhan Red (China). Therefore, it is highly essential to conduct more researches on the exploration of genetic variation under anaerobic condition during germination from diverse rice genotypes [24]. Many genetic studies have been carried out with more intensity even thereafter (following the study of [23]) to unravel the molecular mechanisms underlying AG [98]. Yet, some AG potential varieties have been identified by other workers and the identified genotypes were used in genetic studies and breeding [19, 43, 98-100]. A total of 88 lowland rice landraces were characterized based on morpho-physiological variants under anaerobic condition and three rice landraces (Bausaganthi, Patadhan, Basantichudi) were observed to have superior anaerobic germination potential compared to other rice genotypes [33]. The screening and inherent genetic diversity of 107 rice genotypes were carried out under anaerobic condition for 14 days and several promising flooding tolerant genotypes during germination were identified [11, 101].

3.2. Genetic Resources for Flash Flooding Tolerance

Screening of rice genetic resources for flash flooding tolerance was started in the 1970s at IRRI, Philippines [102]. Though IRRI has maintained 1,00,000 rice genotypes in their germplasm bank, less than 1000 of such genotypes are brought from areas affected by flood. Maximum numbers of varieties *i.e.*, 443 were collected from Bangladesh followed by 82 rice varieties from Sri Lanka, 42 varieties from India, 34 varieties from Thailand, 25 varieties from Combodia, 22 varieties from Vietnam, 21 varieties from China, 13 varieties from Indonesia, 8 varieties from Myanmar and 42 varieties from other countries [1, 80, 103]. Many rice genotypes were evaluated at IRRI through systematic screening under controlled submerged environments, and the same gave discovery of two robust highly tolerant varieties FR13A and FR43B [1]. These rice genotypes were pure lines selections

from traditional rice landraces of Odisha, India. FR13A and FR43B were selected from farmer's variety 'Dhallaputia' and 'Bhetnasia' respectively. Subsequent evaluation under different environmental conditions in different seasons established the high level of tolerance of FR13A [1, 104]. Since the 70s of the last century till date, FR13A is emerged as most famous and recognized flood tolerant rice variety, which was largely adapted by rice breeders worldwide [56, 80]. Vergara and Mazaredo [102] identified some highly tolerant genotypes (Thavalu, Kurkaruppan, Goda Heenati) from Sri Lanka which showed survival of more than 75%. Those varieties have been tremendously used for crop improvement programmes [1]. Screening of various rice germplasms performed at IRRI revealed that less than 1% of rice genotypes identified as submergence donors and also surprisingly, the frequency of *SUB1A* allele was also found to be low. Likewise, only 0.1% of rice genotypes survived under 12 days of complete submergence after the systematic screening of 15,000 rice germplasm at NRRI, Cuttack [105]. Sarkar and Bhattacharjee [87] in their study suggested that the varieties AC37887, IC258990, IC258830 and AC20431-W could be used in rice breeding programme which might enhance flash flood tolerance and crop productivity in flood-prone areas. Also, they suggested few varieties (INGR08109, INGR08111, INGR08113 and AC42091) which could be utilized for the development of variety tolerant to both submergence and stagnant flooding. A detailed physiological study of 27 indigenous rice landraces and one wild rice relative of West Bengal and Odisha was evaluated by Goswami *et al*. [106], under 14 days of complete submergence. They observed the varying degree of survival percentage (50%-100%) of the rice genotypes after the recovery period and identified three rice genotypes (Meghi, Bhasakalmi and Keralasundari) with higher submergence tolerance. Study of 90 types of lowland rice belonging to eastern regions of India and selected from the gene bank maintained by CRRI, Cuttack, Odisha, India, Pradhan *et al.,* [107] screened them for 14 days of submergence. They concluded that the identified highly tolerant genotypes, such as FR 13A, Khoda, CR Dhan 300, Savitri-Sub1, IR 64-Sub1, IC568009 and IC568842 can be used as donor parents in flood tolerant breeding programs. An excellent screening facility for submergence tolerance is available at NRRI, Cuttack since 1978-79 [107]. So far, 7085 different rice germplasms were screened for complete submergence at NRRI, Cuttack, out of which 99 varieties were found to have more than 80% of survival and categorized under tolerant germplasm. A total of 12 rice genotypes could survive under complete submergence for a period of 3 weeks and they are reported to be highly tolerant genotypes. In this aforesaid study, 124 and 6852 number of rice varieties were classified as medium tolerant (having 60-79% of survival rate) and susceptible category, respectively [108]. The possibility of using 'chlorophyll fluorescence' as a screening tool for submergence tolerance was studied by Panda *et al.* [74, 109] and by taking 20 *indica* rice genotypes. Iftekharuddaula *et al.* [110] identified five new submergence tolerant genotypes (DSL-78-8, DG1-349, Putidepa, Kalojoma and Damsi) with unique *Sub1*-region alleles. As many as 88 indigenous rice landraces of Koraput region of Odisha were carried out after keeping them under complete submergence for 14 days and five rice landraces such as Samudrabali, Basnamundi, Gadaba, Surudaka and Dokarakuji were identified as highly tolerant to submergence [46].

3.3. Genetic Resources for Stagnant Flooding Tolerance

So far, very few studies have been carried out for evaluating of stagnant flooding tolerance in rice. A study was conducted by Vergara *et al.* [83], taking 626 rice accessions for investigation over 3 years under stagnant flooding condition and identified some rice genotypes that were tolerant to stagnant flooding. Genotypic differences were observed between 577 genotypes under stagnant flooding in a field trial study, and it was reported that the submergence tolerant genotype FR13A and FR43B did not show good performance under stagnant flooding [111, 112]. Variation in grain yield and other agronomic traits were observed by Amante [113] from the evaluation of 25 genotypes under stagnant flooding. Mallik *et al.* [114] found that the genotypes with limited elongation exhibited higher survival and better yield performances under stagnant flooding stress. Some of the potential breeding lines with both stagnant flooding and submergence tolerance were identified under the 'rainfed lowland breeding programme' at IRRI [115]. Multiple surveys were conducted and as many as 400 rice varieties were collected from eastern states of India. Out of the same in-depth morpho-physiological study of 16 rice genotypes was done for stagnant flooding and it revealed the genotypes AC39416A, AC85, AC34280, Sabita, AC736 and AC443 exhibited a stronger stability index in crop yield under stagnant flooding condition [84]. Screening of rice germplasm for stagnant flooding tolerance was also carried out at IRRI for identification of suitable tolerant genotypes [83, 88]. Eighty elite rice genotypes were screened under stagnant flooding where some of the *Sub1* introgressed high yielding varieties were identified as tolerant to stagnant flooding than the reference genotype without *Sub1* [116]. The National Rice Research Institute (NRRI), Cuttack, has made significant efforts towards screening as well as characterization of rice germplasms, development of rice varieties and cultivation technologies for stagnant flooding tolerance in rice since 1960. Different scientists contributed immensely for the identification of rice genetic resources under stagnant flooding (medium-deep to semi-deep-water depth conditions) through various experiments [117]. Several researchers at NRRI have screened a total of 1005 rice germplasms under stagnant flooding condition and identified 35 number of rice genotypes (having more than 75% of yield stability), 48 number of moderately tolerant varieties (having more than 50% and less than 75% of yield stability) and 922 number of susceptible rice varieties [118].

4. GENETIC BASIS OF FLOODING TOLERANCE IN RICE

The genetic basis for flooding tolerance in rice has been well studied in the last two decades. By the use of molecular biology and molecular marker, technologies enable a way to

identify different QTL and fine mapping of the flooding tolerance genes. A list of different QTLs identified in rice chromosomes and their mapping population for tolerance to different kinds of flooding are presented in Table **2**.

4.1. QTLs for Flooding Tolerance During Germination

Breeding for enhanced AG potential and seedling vigour under flooding during germination have been tried by several researchers in the last three decades [27-29, 32, 119], but with limited success because of complex genetic backgrounds, lack of effective screening method, *etc.* A highly tolerant donor from Myanmar 'Khao Hlan On' was crossed with 'IR 64', a widely grown high yielding rice variety, as a recurrent parent. The resulting BC_2F_2 population was investigated for anaerobic germination potential [23]. In this study, five different QTLs were identified, one each on chromosome number 1 (*qAG1.2*); 3(*qAG3.1*) and 7(*qAG7.2*) and two QTLs on chromosome number 9 (*qAG9.1*) and (*qAG9.2*), explaining phenotypic variation from 17.9 to 33.5%. The largest QTL (*qAG9.2*) was located on the long arm of chromosome 9, with the highest phenotypic variation of 33.5% and LOD score of 20.3. The effect of this major QTL was confirmed and fine mapped to a 50 kb genomic region. Subsequently, cloning and functional validation of the gene encoding a trehalose-6-phosphate phosphatase gene (*OsTPP*) underlying the QTL (*qAG9.2)* has been carried out [120]. The *OsTPP* gene is associated with the metabolism of trehalose-6-phosphate (T6P), facilitating starch mobilization and rapid coleoptiles elongation under anaerobic condition, leading to enhanced tolerance to flooding during germination [80, 121]. This *qAG9.2* QTL has also been introgressed to high-yielding rice genotypes [100]. Several other studies mapping this QTL have focused on AG potential in rice [43, 97, 122, 123]. In the recombinant inbred lines of Kinmaze/D-V85, Jiang *et al.* [97], identified five QTLs, one on each chromosome 1, 2, 7, and two QTLs on chromosome number 5. In this study, three pairs of epistatic loci were also located on chromosomes 2, 3, 5 and 11 whereas the phenotypic variance was found to be 10.5-19.6%. In another study using population (USSR5/N22) Jiang *et al.* [123] observed two QTLs on chromosome number 5 and 11, which had a phenotypic variance in the range of 11-15.5%. Major QTLs were also identified from the tolerant Chinese variety Ma-Zhan (Red), and chromosome 7 was found to have the largest QTL in addition to two smaller QTLs [43]. Baltazar *et al.* [122] studied the QTLs derived from Nanhi (aus landrace), where it was observed that the largest QTL was also located on chromosome number 7. A total of four QTLs (*qAG7.1, qAG7.2 and qAG7.3* on chromosome 7 and *qAG3 on* chromosome 3) were derived from IR64/Kharsu 80A $F_{2:3}$ mapping population with phenotypic variance and LOD value ranging from 8.1 to 12.6% and 5.7 to 7.7 respectively [124]. Additionally, by using 5291 SNP markers in 432 *indica* varieties through genome-wide association (GWAS) study and analyzing expression profiles, Zhang *et al.* [125] observed the LOC_Os06g03520 gene is responsible for flooding tolerance during the germination and identified a total of 15 loci in their study. The combination of GWAS analysis and bi-parental QTL mapping permitted various workers for the identification of a genomic stretch bearing hexokinase gene (HXK6, LOC_Os01g53930), which is linked to elongation of coleoptile in anaerobic rice plants and identified 88 loci linked with AG potential [126]. The same research groups also carried out RNA-sequence analysis of 6 rice varieties, showing a difference in the rate of coleoptile elongation under anoxic state/environment [127]. Yang *et al.* [128] detected 25 loci associated with anaerobic germination across two cropping seasons from 192 recombinant inbred lines (RILs) acquired from a cross between YZX (*indica* cultivar) and 02428 (*japonica* cultivar) by using a high-density bin map composed of 2711 bin markers. Further in this study, 88 differentially expressed candidate genes were identified from 13 stable loci through GWAS of the parents at three crucial stages. A cross of 'Kalarata' with two recurrent parents - 'NSIC Rc222' and 'NSIC Rc238' derived two mapping populations which were screened under anaerobic condition and several QTLs were detected along with three large QTLs [129]. A novel QTL (*qACE3.1*) was identified for coleoptiles elongation under anaerobic condition in the population of chromosome segment substitution lines ($CSSL_S$) substituted with Koshihari in IR64 genetic background [130]. Three QTLs (*qAG1*, *qAG3* and *qAG11*) were identified from a study carried out by Jeong *et al.* [131] by using 188 RILs from a cross between PBR (Photo-blastic Rice) as a donor and 'Nampyeong', a Korean *japonica* cultivar. Among different anaerobic germination QTLs identified till now, the QTL (*qAG.9.2*) is pinned down to *AG1* gene, responsible for coleoptile elongation during anaerobic germination. The detailed biological mechanism of this important QTL so far is not clear [132], and the same requires further study.

Table 2. List of QTLs identified in rice chromosomes and their mapping population with flanking marker, logarithm of odds score (LOD) and phenotypic variance explained (PVE) for tolerance to different types of flooding.

Types of Flooding	Mapping Population	QTLs	Chromosomes	Flanking Marker	LOD Value	PVE (%)	References
Flooding during germination	F_2(USSR5/N22)	*qAG5*	5	RM405-RM169a-RM249	2.97 to 3.78	11 to15.5	[123]
		qAG11	11	RM21-RM254a-RM224	2.97	10.99	
	RIL(Kinmaze/DV85)	*qAG1, qAG2, qAG5a, qAG5b, qAG7*	1, 2, 5, 7	-	-	10.5 to 19.6	[97]

(Table 2) contd....

Types of Flooding	Mapping Population	QTLs	Chromosomes	Flanking Marker	LOD Value	PVE (%)	References
	BC_2F_2(Khaiyan/IR64)	*qAG1*	1	RM312	3.66 to 5.71	12 to 29.24	[193]
	-	*qAG2.1*	2	RM341	-	-	
	-	*qAG11*	11	RM206	-	-	
	-	*qAG12*	12	RM28759	-	-	
	BS_2F_2(Khao Hlan On/IR64)	*qAG1.2*	1	RM11125-RM104	5.69 to 20.34	17.9 to 33.5	[23]
	-	*qAG3.1*	3	RM7097-RM520	-	-	
	-	*qAG7.2*	7	RM21868-RM172	-	-	
	-	*qAG9.1,*	9	RM8303-RM5526	-	-	
	-	*qAG9.2*	9	RM3769-RM105	-	-	
	BC_2F_3(Ma-Zhan (Red)/IR42)	*qAG2,*	2	RM263-RM5378	-	-	[43]
	-	*qAG5,*	5	RM5361	-	-	
	-	*qAG6*	6	RM204-RM402	-	-	
	-	*qAG7.1,*	7	RM3583-RM21427	-	-	
	-	*qAG7.2,*	7	RM7338-RM346	-	-	
	-	*qAG7.3*	7	RM21803-RM234	-	-	
	$F_{2:3}$(Nanhi/IR64)	*qAG2.1*	2	id2001831-id2003094	2.16 to 13.93	14.1 to 18.3	[122]
	-	*qAG2.2*	2	id2006621-id2007526	-	-	
	-	*qAG3*	3	id3007932-id3010875	-	-	
	-	*qAG7*	7	wd7000465-id7002784	-	-	
	-	*qAG11*	11	id11009201-id11010245	-	-	
	$F_{2:3}$(IR64/Kharsu 80A)	*qAG3*	3	id3002377-id3004190	5.7 to 7.7	8.1 to 12.6	[124]
	-	*qAG7.1*	7	id7000519-id7002260	-	-	
	-	*qAG7.2*	7	id7002427-id7003359	-	-	
	-	*qAG7.3*	7	id7003853-id7004429	-	-	
	RIL(PBR/Nampyeong)	*qAG1*	1	SNP-1.25043823- 863795	3.06 to 5.69	6.71 to 14.52	[131]
	-	*qAG3*	3	2495249- 2497338	-	-	
	-	*qAG11*	11	10922039- SNP-11.3839501	-	-	
	RIL(YZX/02428)	*qCD.1*	1	mk258-mk259	5.15	9.73	[128]
	-	*qCV.2*	2	mk312-mk313	2.80	5.19	
	-	*qCD.2.1*	2	mk368-mk369	4.95	9.26	
	-	*qCD.2.2*	2	mk375-mk376	5.54	8.72	
	-	*qCSA.3*	3	mk589-mk593	4.40	10.35	
	-	*qCD.3.1*	3	mk623-mk624	5.63	9.09	
	-	*qCD.3.2*	3	mk646-mk647	5.84	9.81	
	-	*qCL.3.2*	3	mk818-mk819	2.67	4.99	
	-	*qCD.4.1*	4	mk1005-mk1006	2.85	4.28	
	-	*qCL.4.1*	4	mk1033-mk1034	2.81	6.04	
	-	*qCL.4.2*	4	mk1047-mk1052	3.30	6.44	
	-	*qCD.4.2*	4	mk1063-mk1064	3.52	6.46	
	-	*qCD.5*	5	mk1219-mk1220	3.52	5.32	
	-	*qCL.6*	6	mk1329-mk1330	2.69	6.02	
	-	*qCSA.6*	6	mk1402-mk1406	3.67	8.65	
	-	*qCV.6.2*	6	mk1426-mk1427	6.56	12.65	
	-	*qCV.6.3*	6	mk1489-mk1490	3.82	7.30	
	-	*qCD.7*	7	mk1758-mk1759	2.86	5.16	
	-	*qCV.8*	8	mk1886-mk1887	2.60	4.84	

(Table 2) contd....

Types of Flooding	Mapping Population	QTLs	Chromosomes	Flanking Marker	LOD Value	PVE (%)	References
Flash flooding	F_2(IR40931-26/PI543851)	*SUB1*	9	-	36.9	69	[133]
	F_2:F_3(Madabaru/IR72)	*qSUB1.1,*	1	MDC17-RM12168	11.2	52.3	[98]
	-	*qSUB2.1,*	2	RM6318-RM2578	4.1	36.4	
	-	*qSUB9.1,*	9	RM23911-RM23966	3.6	18.6	
	-	*qSUB12.1*	12	RM511-RM463	3.5	16.3	
	RIL(FR13A/IR74)	-	6,7,9,11,12	-	-	-	[134]
	F_1, DHL(IR49830-7-1-2/CT6241-17-1-5-1)	-	9	-	-	-	[140]
	BC_4F_3(IR67819F2-CA-61/KDML105)	-	9	-	-	-	[139]
	RIL(IR42/FR13A)	*qSUB1.1,*	1	id1000556-id1003559	5.0	20.20	[138]
	-	*qSUB4.1*	4	id4010621-id4012434	3.0	12.40	
	-	*qSUB8.1*	8	id08005815-id8007472	3.1	13	
	-	*qSUB9.1*	9	id9001352-SC3	36.9	69	
	-	*qSUB10.1,*	10	id10005538-RM25835	3.9	15.80	
Stagnant flooding (medium depth)	RIL(Chiherang-Sub1/IR10F365)	*q GW1.1*	1	214137-id1007975	4.36	8.7	[166]
	-	*q GW5.1*	5	5428382-ud5000983	4.07	8.3	
	-	*q GW10.1*	10	10603169-10703329	6.30	13.1	
	-	*q GW10.2*	10	9958372-id10003608	4.14	9.0	
	-	*q DTF1.1*	1	801364-id1016674	3.08	6.0	
	-	*q DTF3.1*	3	2499734-2560888	12.50	26.0	
	-	*q DTF5.1*	5	5515384-id5013231	4.11	7.0	
	-	*q DTF10.1*	10	id10002842-10586997	5.22	9.0	
	-	*q FLW3.1*	3	2499734-2560888	4.00	11.3	
	-	*q FLL4.1*	4	id4000574-4295290	4.11	9.3	
	-	*q FLL5.1*	5	ud5000983-5747652	6.18	14.0	
	-	*q FLL9.1*	9	9592671-id9007287	2.94	13.0	
	-	*q GY3.1*	3	2499734-2560888	6.20	14.3	
	-	*q GY5.1*	5	id5003312-ud5000983	3.66	12.2	
	-	*q GY6.1*	6	id6000402-5903052	3.46	7.4	
	-	*q HI2.1*	2	1489783-1845605	3.41	72.4	
	-	*q HI5.1*	5	id5003312-5515384	3.34	72	
	-	*q HI7.1*	7	7768382-7949610	8.67	20.4	
	-	*q HI7.2*	7	7102234-id7002749	4.65	10	
Stagnant flooding (deep water)	F_2(Habiganj Aman VIII/ Patnai23)	$QTL_{CHR\ 1}$	1	RM128-RM104	3.8	0.09	[192]
	-	QTL_{CHR12}	12	RM5479-RM6953	18.2	0.41	
	F_2(Bhadua/Taichung 65)	*qLEI3*	3	XNpb144-RM8208	9.0	40.7	[89]
	-	*qLEI12*	12	RM5479-f112163	11.7	38.5	
	BC_4F_2(W0120/T65)	*qTIL12*	12	RM6368	5.89	36	[156]
	-	*qNEI12*	12	M2	4.47	27	
	-	*qLEI12*	12	RM6386	5.63	26	
	F_2(Bhadua/Taichung 65)	*qRIE1*	1	XNpb113-G54	7.5	30.6	[89]
	-	*qRIE12*	12	RM5479-f112163	5.3	22.2	-
	RIL (T 65/Bhadua)	*qTIL 2*	2	RM208	4.9	14.4	[164]
	-	*qTIL 4*	4	RM2439 -RM1388	3.4	7.9	

4.2. QTLs for Flash Flooding Tolerance in Rice

Molecular mapping by Xu and Mackill [133] led to the discovery of major QTL '*Submergence 1 or Sub1*' on chromosome number 9, which regulates the submergence tolerance, derived from FR13A parent [77, 134, 135]. This robust QTL had a significant LOD score of around 36% and contributed 69% of total phenotypic variation for submergence tolerance [49, 77, 133, 135-137]. Thereafter, several other studies confirmed that *Sub 1* QTL is the contributor for submergence tolerance [13, 99, 135] and located other minor QTLs which contributed less than 30% of phenotypic variation for tolerance [134, 138-140]. This may be due to the tolerance mechanisms possessed by these QTLs are unlike *Sub1*. This proposition needs further investigation to confirm and authenticate the same [19]. *Sub 1* was further mapped to a 0.16cM region on chromosome number 9 with 3000 F_2 progeny [141]. Subsequently, Xu *et al.* [13], by a fine-scale physical mapping study, narrowed the locus down to 0.075 cM using 4022 F_2 individuals. The *Sub 1* locus represents a group of three genes *Sub 1A, Sub 1B, Sub 1C,* which encodes for Group VII apatala2/ethylene responsive factor (ERF) [13, 142]. *Sub 1B,* and *Sub 1C*genes are present in all accessions of *Oryza sativa,* whereas *Sub 1A* occurs only in submergence tolerant rice genotypes [13, 56, 143]. Studies pertaining to sequence variation in protein-coding regions of *Sub 1A* revealed the existence of two alleles, *Sub-1A-1* tolerant allele and *Sub1A-2* intolerant allele [143]. Thus, it has been proved that *Sub1A-1* is a primary determinant for submergence tolerance in rice [13, 135]. Septiningsih *et al.* [98] found four new QTLs located on chromosome number 1, 2, 9 and 12 in $F_{2:3}$ population when cross was made between two moderately submergence tolerant rice varieties *i.e.* IR72 and Madabaru. Four hundred sixty-six families were phenotyped under submerged conditions from the $F_{2:3}$ populations and a subset of 80 families were chosen from the two extreme sides for the QTL analysis. Kurokawa *et al.* [144], identified the gene '*Leaf Gas Film1'* (*LGF1/OsHDS1*) which is mainly responsible for surface hydrophobicity and retention of leaf gas films on flooded rice leaves. It contributes greatly to the underwater gaseous exchange and thereby increases the flooding tolerance in rice [66, 75, 145]. The discovery of this gene further gives an opportunity for understanding the variations present in different rice varieties in respect of its ability to retain the gas film [146] as well as the possibility of identification of alleles which confer a higher expression of *LGF1/OsHSD1* gene.

4.3. QTLs for Stagnant Flooding Tolerance

Among different kinds of flooding, deepwater rice drew the initial attention and was noticed by rice breeders because of its unique shoot elongation ability. Ramiah and Ramaswami [147] studied the inheritance pattern of stem elongation in deepwater rice and for the first time, they reported that the duplicate genes are classified as elongation factor (*ef1* and *ef2*) regulated elongation of internode. Hamamura and Kupkanchankul [148] published the partial dominance and involvement of five to six genes regulating the floating ability of deepwater rice varieties by using di-allele crosses and analysing the progeny for submergence tolerance. Further, the measurement of total internode length and use of the position of the lowest elongated internode for the evaluation of deep-water characters are widely supported by several authors [149, 150]. The study of Tripathi and Rao [151] revealed that a single dominant gene was responsible for early nodal differentiation. However, Suge [152] described that the elongation of internode was regulated by the action of complementary genes. From the study of Eiguchi *et al.* [153] it was observed that '*dw3*' (single recessive gene) modulate internode elongation in case of deepwater rice genotypes. Sripongpangkul *et al.* [154] carried out QTL analysis using RILs from a cross between IR74 and Jalmagna to study the mechanism of stem elongation in case of deepwater rice by using the QTL. From this study, a total of 26 QTLs were detected which regulated the plant elongation as well as submergence tolerance. Nemoto *et al.* [155] identified two QTLs for the lowest elongation internode trait on chromosome numbers 3 and 12. Similarly, Kawano *et al.* [89] performed QTL analysis by using the lowest elongated internode and internode elongation rate as parameters and identified 2 QTLs for each of the parameter on chromosome number 3 and 12, and 1 and 12 respectively. Hattori *et al.* [156] carried out QTL mapping studies by using three parameters (lowest elongation internode, total internode length, the number of elongated internodes) in three different populations. This study revealed that Quantitative Trait Locus positions detected in various populations were found in similar genomic regions on chromosome number 1, 3, 12, suggesting the importance of these QTLs in deepwater rice for elongation response. Hattori *et al.* [157] reported the effect of internode elongation by producing near-isogenic lines (NIL) on the genetic background of Taichung65 *i.e.* NIL-1, NIL-3, NIL-12 and reported QTL on chromosome number 12. This QTL was found to be most important for internode elongation in deepwater rice varieties. Further, Hattori *et al.* [90] discovered two ethylene response factor genes (*Snorkel1* (*SK1*) and *Snorkel2* (*SK2*)) by positional cloning and functional analysis in the QTL regions of chromosome number 12. Also, it was studied that these genes were absent or non-functional in non-deepwater rice (for example Taichung65), including all *japonica* varieties [90]. These *SK* genes were highly expressed in the sheath, leaf blade and the basal part of the stem which includes the nodes as well as internodes. During the internode elongation, an enhanced level of expression of 'expansin' which is associated with cell wall softening [158-160] and a shift in the orientation of cellulose microfibrils was noticed [161]. The formation of aerenchyma in the internode occurs together with its elongation and is accelerated by ethylene [162, 163]. Nagai *et al.* [164] investigated total internode elongation at the initial seedling stage and detected 2 QTLs such as *qTIL2* and *qTIL4*. A genome-wide eQTL (expression quantitative trait loci) mapping based on a microarray platform was performed by using 85 RIL populations from a cross between 'Taichung 65' and 'Bhadua'. The authors identified 10,047 eQTLs in the study, which were majorly found on chromosome numbers 1, 4

and 12 [165]. A QTL mapping study linked with stagnant flooding was carried out by Singh *et al.* [166], using 148 recombinants inbreed lines which were obtained by crossing 'Ciherang-Sub1' and 'IR10F365'. Some major QTLs were detected for yield component traits and other agronomically important characters under stagnant flooding condition at IRRI and will be further validated as targets for molecular studies and molecular breeding [80]. Although multiple QTLs has been identified in this regard by different research groups, the *SK1* and *SK2* still remain as the most effective QTLs for internode elongation in deep water rice. Again more QTL mapping studies are needed for medium depth stagnant flooding condition since there is no prominent QTL identified for yield stability under these conditions.

5. MARKER-ASSISTED BREEDING APPROACHES FOR THE DEVELOPMENT OF FLOODING TOLERANCE IN RICE

Molecular marker-assisted selection is a strategy for boosting up the crop improvement programs for different abiotic and biotic stress tolerance [167-170]. In recent times, marker-assisted backcrossing (MABC) is one of the most widely used breeding programs. The purpose of MABC is mainly to incorporate the target QTL from agronomically non-standard donors into mega varieties and to obtain genotypes with stress tolerance. This strategy is more accurate and efficient than the earlier conventional breeding approach [171]. The discovery of *Sub1* gene laid the foundation of marker-assisted selection for flooding tolerance [13, 51, 56, 142]. List of popular *SUB 1* incorporated mega varieties developed through marker-assisted back crossing (MABC) for submergence tolerance was presented in Table **3**.

5.1. Breeding Approaches for Flooding Tolerance During Germination

The molecular breeding for AG potential in rice was started with the identification of *AG1* QTL, derived from Khao Hlan On [120]. The major QTL *qAG9.1* has been successfully incorporated into some mega rice varieties or their *Sub1* lines such as IR64, PSB Rc18-Sub1 and PSB Rc82, IR64-Sub1 [43, 56, 100]. Similarly, the introgression of *AG2* locus derived from Ma-Zhan Red to elite high yielding varieties gathered more importance to concentrate and the work has been in progress [142]. Toledo *et al*. [100] studied the introgression of *AG1* locus into Ciherang-Sub1 variety through MABC by using IR64-AG1 (a closely related donor). In this study, the *AG1* incorporation and Ciherang genome restoration was performed in two backcross generation and thereafter one generation of self-pollination was carried out. Four *japonica* type breeding lines were developed from a cross of a Korean *japonica* rice variety 'Dongan' and 'Khao Hlan On' (anaerobic germination tolerant donor from Myanmar) through marker assisted selection approach [172].

5.2. Breeding Approaches for Flash Flooding Tolerance in Rice

After identification and isolation, the *Sub1* gene was incorporated into mega rice varieties through MAB (marker-assisted backcross) approach [54, 99, 110, 135, 173-176]. The development of molecular markers for the *Sub 1* genomic region allowed the precise transfer of this QTL for an effective breeding program [98, 143, 175]. Till date, several popular submergence tolerant mega rice varieties have been de-

Table 3. List of popular *SUB1* incorporated mega varieties developed through marker-assisted back crossing (MABC) in different countries.

SUB1 Incorporated variety	Donor Parent	Recurrent Parent	Origin	Generation	Year of Release	References
Swarna-Sub1	IR49830	Swarna	India	BC_3F_2	2009-2010	[110, 142, 175]
BR11-Sub1	IR49830	BR11	Bangladesh	BC_2F_2	2010	[110]
IR 64-Sub1	IR40931	IR 64	Philippines	BC_2F_2	2009	[177]
Samba-Mahsuri- Sub 1	IR49830	Samba Mahsuri	India	BC_2F_2	2011, 2013	[177]
Thadokkam1-Sub1/ TDK1-Sub1	IR40931	Thadokkam1/TDK1	Laos	BC_3F_2	2017	[137, 173]
CR1009-Sub1	IR40931	CR1009/Savitri	India	BC_2F_3	2017	[56]
PSB Rc 18-Sub1	IR 64-Sub1	PSB Rc 18	Philippines	BC_1F_2	2017	[80, 178]
Ciherang-Sub1	IR49830	Ciherang	Indonesia	BC_1F_2	2012 2013	[80, 178]
Gayatri-Sub1	IR49830	Gayatri	India	BC_2F_3	2016	[108]
Sarala-Sub1	IR49830	Sarala	India	BC_2F_3	2016	[108]
Varshadhan-Sub1	IR49830	Varshadhan	India	BC_2F_3	2016	[108]
Pooja-Sub1	IR49830	Pooja	India	BC_2F_3	2016	[108]
Pratikshya-Sub1	IR49830	Pratikshya	India	BC_2F_3	2017	[108]
AS996-Sub1	IR40931	AS996	Vietnam	BC_1F_2	2016	[56, 194]
Bacthom 7-Sub1	IR40931	Bacthom 7	Vietnam	BC_1F_2	2016	[195]
KDML 105-Sub1	IR40931	KDML 105	Thailand	BC_1F_2	2017	[139, 183]

veloped by using *Sub1* gene such as IR64-Sub1, Swarna-Sub1, Thadokkam1-Sub1, BR11-Sub1, Samba Mahsuri-Sub1, *etc.* These high yielding *Sub1* incorporated mega varieties are promoted for large scale cultivation in Asia and Africa to make them commercially viable [54, 173, 177]. Septiningsih *et al.* [178] reported that *Sub1* gene was incorporated into 2 other genotypes *i.e.* 'PSB-RC18' from Philippines and 'Ciherang' from Indonesia. Recently the *Sub1* gene was also incorporated into ten regionally adapted highly popular rice genotypes of India [80, 179, 180]. Presently the IRRI and the National Breeding Programme in other countries of Asia are incorporating the *Sub1* gene into many prominent rice varieties [1]. The results of various screenhouse and field trials evaluation (both on-station and farmer's fields) of these improved elite varieties exhibited a higher capacity to survive in complete submergence than their recurrent parents. Again, *Sub1A* did not show any adverse effect on other agronomically important traits [54, 56, 76, 135, 139, 177, 181-183] and within a short period, these prominent varieties have become popular among the farmers [174]. *Sub1* incorporated lines exhibited a yield gain of 1-3.5 t/ha^{-1} than their non-*Sub1*counterparts, depending upon the growth stage and flooding duration [62]. The *Sub1* incorporated varieties exhibited minimum elongation with better survival, quicker recovery after complete submergence, earlier flowering and maturity, retention of better grain quality and other desirable agronomic traits as compare to their non-*Sub1* counterparts through different studies [54, 80, 135, 175, 177, 184, 185]. Presently over four million rice farmers are cultivating *Sub1* rice in Asia [48, 51]. The history of utilisation of FR13A in breeding programs for the development of SUB1 mega rice varieties is represented in Fig. (**2**).

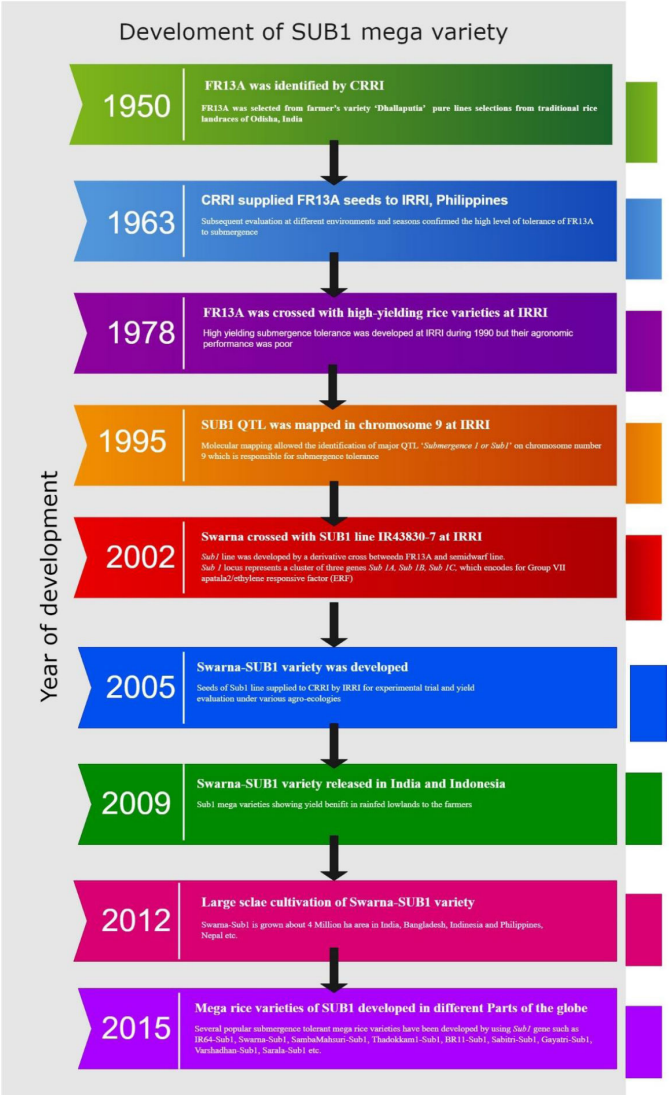

Fig. (2). Time line of utilization of FR13A, a miracle of rice germplasm tolerance to submergence for the development of *SUB1* mega rice varieties. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

5.3. Breeding Approaches for Stagnant Flooding Tolerance in Rice

The progress of breeding programme for improvement of rice genotypes tolerance to stagnant flooding is underway [116]. From 'IRRI 154' (an identified genotype for stagnant flooding tolerance), a RIL population has been constructed for QTL mapping [142]. IRRI, Philippines, in collaboration with India and other countries like Bangladesh and Nepal has found out and evaluated new breeding lines to bring out improvement in the tolerance ability of rice genotypes under stagnant flood situations [80, 115]. A field evaluation was performed with *Sub 1* introgressed varieties under stagnant water flooding by Singh *et al.* [81], in which the *Sub 1* rice varieties showed a decrease in yield as well as survival; as *Sub 1 gene* restricts growth under complete submergence stress. Kuanar *et al*. [186], investigated the response of *Sub1* incorporation into high yielding rice cultivars by comparing the *Sub1* incorporated and parental lines of 'Swarna' and 'Savitri' under stagnant flooding condition. They reported that the *Sub 1* incorporation in to the mega cultivars increase sensitivity to stagnant flooding.

CONCLUSION AND FUTURE PROSPECTS

Although remarkable progress has been achieved through MABC approaches for the development of submergence tolerant mega rice varieties, however, we still have several critical problems to overcome molecular breeding of flooding tolerance in rice. In recent times, the intensity and duration of flooding are increasing due to the extreme weather events aggravated by climate change scenarios. The available *SUB1* incorporated mega varieties sensitive to stagnant flooding and not providing yield stability in different flooding regimes. So, it is necessary for finding a superior allele other than *SUB1A* gene or novel genes that may give even better tolerance and yield stability to flooding stress. And also, attempts should be made for developing superior high yielding varieties by pyramiding the *AG*, *SUB1* and *SK* genes into a single elite cultivar that could survive under diverse flooding regime and improvement of yield stability in a rainfed agroecosystem. Since the rainfed lowland areas are prone to multiple abiotic and biotic stress, breeding varieties resilient to multiple stresses can be accomplished by combining *SUB1* with other tolerant traits or genes for wider adaptation in the less favourable rice ecosystem. Advancement in the emerging technologies pertaining to molecular genetics, genomic tools and breeding approaches can be used as an integrated manner for the improvement of flooding tolerance in rice.

CONSENT FOR PUBLICATION

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CONFLICT OF INTEREST

The authors declare no conflict of interest financial or otherwise.

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