A Critical Review of Submergence Tolerance Breeding beyond Sub 1 Gene to Mega Varieties in the Context of Climate Change

Dev Nidhi Tiwari
Senior Scientist
National Rice Research Program
Hardinath, Dhanusha
Nepal

ABSTRACT

Flash flood, stagnant flooding and anaerobic germination are various forms of submergence that occurs at different stages of rice growth causing significant damage to crop production for more than 15 millions poor farmers in the rainfed lowland region of South and Southeast. Before the discovery of Sub 1 gene farmers had to rely on low yielding, submergence-intolerant varieties that incurred yield drastic reduction to complete failure of the crop every year. With the discovery of major quantitative trait loci (QTL) submergence 1 (Sub 1) which is responsible for this trait, submergence tolerance breeding has achieved its milestone to overcome the burning issue. Cloning and isolation of SUB1 locus in popular submergence tolerance parent FR13A that led to the identification of ethylene-responsive factor (ERF) gene SUB1A-1 that is responsible for submergence tolerance. The Sub 1 QTL is a single gene that has the LOD score of 36 which explained phenotypic variance of 69% conferring tolerance to complete submergence of two weeks. The submergence -1 (Sub-1) locus representing a cluster of three ethylene responsive factor (ERF) genes: sub1A, sub1B and sub1C. Identification of the SUB1 gene was the entry point for enabled marker assisted selection (MAS) for submergence tolerance. Popular varieties also are known as mega varieties which possessed high yielding and good grain quality was used as the recurrent parent in marker assisted backcrossing (MABC). Beyond the Sub 1 varieties, the present day rice breeders paid attention to tolerance to stagnant flooding and tolerance to anaerobic germination under deep water and flash flood during seedling germination respectively. Quantitative Trait Loci (QTLs) have been identified for anaerobic germination also referred to as AG (AG1 and AG2) and stagnant flooding for deepwater rice (SNORKEL1 and SNORKEL2). Furthermore, the combination of both traits conferring tolerance to stagnant flooding with Sub 1 or Sub 1 with anaerobic germination (AG) is the future direction of rice breeding through gene pyramiding approach to develop the rice varieties tolerant to multiple stresses to enhance yield and quality to combat the future challenge of food and nutritional insecurity.

Keywords: Submergence, Flash Flood, Stagnant Flooding, Anaerobic Germination, Marker Assisted Backcrossing.

INTRODUCTION

Flooding is a major abiotic stress and leading constraint limiting the crop production for the rice growers basically in the rainfed lowland areas and irrigated areas where flash flood and deepwater conditions prevails for few weeks to longer [20], [30]. Around 40 millions hectares of rice growing areas are affected by drought and flooding stress at different forms and intensities ad various growing stages [9]. Both of these major stresses are common phenomenon in the rainfed lowland ecosystem almost in same growing areas within same season. Submergence stress is mainly caused by flash flood during the monsoon season with varying intensity and periods. The flash flood inundates the rice fields completely at the early stage before or immediately after the crop establishment for few days to weeks. When rice is submerged for more than five days the crop dies and cannot recover from the stress after water is receded [30]. The farmers who experience flash floods every year cultivate tall and submergence tolerant local varieties that are mostly low yielding in nature. In some cases farmers even have high yielding but submergence-intolerant landraces usually suffer from crop failure or massive yield reduction due to occurrence of flash flood. In the lowland areas the
flood water remains in the rice field for more than two weeks to several months. In such a circumstances, water level reaches 20-50 cm in depth. Such a phenomenon is commonly known as stagnant flooding [28], [20], [35], [30]. In such a situation, rice production also reduced due to poor tillering and highly prone to lodging [37], [35], [30]. In some areas, stagnant flooding is immediately followed by flash flood where farmers have only option to grow their locally adapted landraces that are capable of avoiding the stress even though they are poor yielding. Similarly, in low lying areas where water level remain for longer period and reached upto height of the crop, farmers cultivate floating rice or deepwater rice that have capacity of internode elongation that facilitates the crop to expose leaves and panicles above the water surface [3]. Such deepwater rice have low yield due to excessive vegetative growth. Stagnant flooding is also a kind of submergence stress during which water remains in the field at depths of 50 to 60 cm for up to several months [21], [5]. Stagnant flooding is particular to rainfed lowland areas in Eastern India, Bangladesh, Nepal, Cambodia, Thailand and some parts of Africa.

Submergence is the widespread constraint to more than 15 millions poor farmers of rice growing areas in rainfed lowland region of South and Southeast. In these areas farmers cultivate their own local landrace that can withstand submergence but are basically poor yielders. Likewise, high yielding and submergence intolerant rice varieties that are grown by farmers in large scale have been affected by flash floods frequently. The occurrence of flash floods are triggered by unpredicted and variability in weather factors causing erratic rainfall during the monsoon season. To overcome such situations, some sustainable solutions are required which could be development of high yielding and submergence tolerant varieties that would be widely accepted by farmers in a affected areas [28].

In deepwater and floating rice areas, water stagnates for longer than two weeks and varieties overcome the situation by shoot elongation to cope with inundation [26], [7], [16], [18]. The studies estimated that flood affected area is in increasing trend within this one decade affecting 19 million hectare to 40 million hectare of cultivated land. This type of scenario have been arised due to vulnerable climatic conditions [39], [18]. Flash floods are also causing extensive crop loss at the germination and early seedling stage that leads to poor plant stand i.e. population in aerobic rice fields. It is common in unlevelled land of irrigated system and flood prone rainfed ecosystem in condition where rainfall occurs soon after the seeding rice [14], [1], [30]. Existing rice varieties with farmers donot germinate, grow and survive under inundation and as a result of that seedling establishment is resulted into poor seedling [18]. The occurrence of submergence at the seed germination period impart difficulty to the farmers in adopting the direct seeded rice technology. In such a areas farmers fail to timely cultivate the crop due to lack of such varieties. When crop is damaged by floods immediately after seeding they have no ther alternative either reseed or transplant . It becomes very expensive and costly due to increased labor that affecting the subsequent crop as well [17], [18].

Many efforts were made in the past to develop direct seeded rice varieties with tolerance to flooding during germination however success has not been achieved due to lack of tolerant donor parents and complex trait itself [42], [43], [2], [30]. With rigorous screening of thousands of rice accessions and landraces tolerant donors of submergence during germination were identified and regarded as anaerobic germination [1], [30].

Continued work to develop submergence tolerant varieties, it became essential to combine stagnant flooding tolerance with submergence (based on SUB1). This work was initiated with mega variety Swarna Sub 1 in which both submergence and stagnant flooding were combined with conventional breeding through phenotypic selection. The new variety IRRI 119 was developed by IRRI and released by Philippines as PSB Rc68 [28], [20], [30]. Later on breeding lines with high yielding and stagnant flooding tolerance have also been developed through conventional breeding [20] [30].

2. HISTORY OF SUBMERGENCE BREEDING AND SUB1 BEYOND

A milestone achievement in submergence tolerance breeding was begun with the discovery of major quantitative trait loci (QTL) submergence 1 (Sub 1) which is responsible for this trait [40], [5], [30]. With continued efforts of the plant breeders and biotechnologist cloning and isolation of SUB1 locus in popular submergence tolerance parent FR13A that led to identification of ethylene-responsive factor (ERF) gene SUB1A-1 that is responsible for submergence tolerance [41], [30].

The donor parent of SUB1 gene FR13A, a pure line variety derived from landrace after selection in Dhalputta a native landrace from Orissa of India was found as highly tolerant cultivar and later on subsequently used in breeding as tolerant donor. Thereafter many breeding lines have been developed for submergence tolerance, new high-yielding and adapted breeding lines derived from FR13A including IR49830 and IR40931 were developed at IRRI which is highly tolerant and also good yielding [19], [5], [30]. Although this variety is not popular among the farmers for cultivation due to lack of some special traits that present in their preferred variety [24], [30].

After investigation and isolation of Sub 1, through introgression of Sub 1 into farmers preferred widely adopted submergence tolerant mega rice varieties like IR64-Sub 1, Samba Mahsuri-Sub 1, Thadokkamq-Sub 1, BR11-Sub 1 and Swarna Sub 1 are released in Asia and Africa [27], [34], [6], [18].
2.1 Genetics of submergence tolerance in rice

According to [22], submergence tolerance was found to be governed by a single dominant gene. The findings of recent studies on genetic basis of submergence tolerance is controlled by major quantitative trait locus (QTL) on chromosome 9, designated as Sub (T), is responsible for this trait which is derived from the parent FR13A [40], [23], [25], [37], [28]. Sub (T) locus had a remarkable high LOD score of about 36 and accounted for approximately 69% of the phenotypic variation for the trait [40], [25], [28] that confers tolerance to complete submergence for two weeks. According to [13] the rice submergence tolerance level is largely controlled by a single gene designated Sub1 which is accounted for 69% of the phenotypic variance of the trait. The submergence tolerance in rice is induced by submergence -1 (Sub-1) locus representing a cluster of three ethylene responsive factor (ERF) genes: sub1A, sub1B and sub1C (Fig. 1) where sub1 genes are member of group of group VII of ERF gene family associated than other rice ERF genes. The two sub1B and sub1C are found in both indica and japonica accessions while sub1A occurs in only indica has been discovered that submergence tolerant rice varieties contain sub1A-1 allele but the susceptible accessions only possess sub1A-2 alleles. Thus it has been believed that sub1A-1 allele is responsible for regulation of submergence tolerance in rice [41], [12], [28].

Figure 1: Sub1 locus organisation in rice (Oryza sativa L.) (Fukao et al. 2009)

The Sub 1 locus has cluster of three genes, encoding ethylene response factors. Two of these genes, Sub1B and Sub1C, are invariably present in the Sub 1 region. In contrast, the presence of Sub1A is variable. A survey identified two alleles within those indica varieties that possess this gene: a tolerance-specific allele named Sub1A-1 and an intolerance-specific allele named Sub 1A-2. Overexpression of Sub1A-1 in a submergence-intolerant O. sativa ssp. japonica conferred enhanced tolerance to the plants, downregulation of Sub1C and upregulation of Alcohol dehydrogenase 1 (Adh1), indicating that Sub1A-1 is a primary determinant of submergence tolerance. The FR13A Sub1 locus was introgressed into a widely grown Asian rice cultivar using marker-assisted selection (MAS). The variety developed from this approach possesses high yield and all the traits similar to recurrent parent and have very good submergence tolerance [41].

Mechanism of submergence response of deepwater rice and lowland rice are contrasting; ‘submergence-escape’ and ‘submergence-tolerance’ (Fig. 2). The ‘submergence escape’ response of deepwater rice is to promote internode elongation under submerged conditions to outgrow submergence The rapid underwater growth is an energy-consuming process which requires the consumption of stored carbohydrates and other energy resources. The submergence escape response is only successful if photosynthetic organs emerge prior to exhaustion of carbohydrate reserves and other energy resources. Indeed, even deepwater rice dies within 14 days of complete submergence [41], [31], [10]. In contrast, the ‘submergence-tolerance’ of lowland rice is mediated by the promotion of shoot elongation and the consumption of carbohydrate reserves during submergence [32] [11] [41] [10]. The tolerant cultivars can survive complete submergence for up to 14 days and can resume the initiation of plant growth upon desubmergence. In the tolerant lowland rice under submergence conditions, ethylene production is low and carbohydrate consumption is also low resulting into reduced elongation of internodes that were mediated by Sub1A which inhibits ethylene response. Plants undergo complete tolerance of submergence for two weeks and after desubmergence plants resume growth by utilizing the reserved carbohydrate [10].
3. BREEDING RICE FOR TOLERANCE TO SUBMERGENCE

3.1 Flash flood tolerance during vegetative stage

After identification of submergence tolerant donor FR13A, many breeders extensively used this variety and unravelled major QTL Sub1 responsible for submergence tolerance. Subsequently, Sub 1 gene was fine mapped using F2 segregating population and underlying genes cloned as a cluster of three ethylene responsive factor (ERF) genes, SUB1A, SUB1B and SUB1C [41]. Furthermore, it was obvious that SUB1A was the mainly responsible for tolerance [41]; later on this finding has been confirmed through a progeny test of recombinants identified within the SUB1 cluster in several thousand individuals in segregating populations [28], [30]. Based on allelic survey of Sub1A it was further revealed that Sub1A-1 is tolerant and Sub1A-2 is intolerant [33], [29]. Identification of the SUB1 gene was the entry point for enabled marker assisted selection (MAS) for submergence tolerance. Popular varieties also known as mega varieties which possessed high yielding and good grain quality were used as recurrent parent in marker assisted backcrossing (MABC). FR13A derived two improved lines were used as donors IR49830-7-1-2-2 (IR49830-7) and IR40931-33-1-3-2 (IR40931-33) [19], [28]. By using precision MABC, the high yield and desirable grain and eating qualities of these mega-varieties were retained [28] [34] [30].

To shorten the breeding period and high throughput three steps of MABC were used: (1) foreground selection, in which markers tightly linked to SUB1 are used to select for the locus; (2) recombinant selection, in which closely linked flanking markers are used to minimize the donor chromosomal segment containing SUB1; and (3) background selection, in which DNA markers are used to accelerate the recovery of the recurrent parent genome (Figure 4), [4].

The method of selecting recombinants on both sides of the target locus in at least two backcross (BC) generations during MABC was first proposed by [44] and applied in rice by Chen and colleagues (2000). Some Sub 1 varieties developed through MABC have been given in the Table 1 and commonly used markers used in development of Sub1 gene is presented in Table 2.
Table 1. Some popular Sub1 varieties developed through MABC

| Recurrent parent | Country of origin | Donor parent | Generation | Introggression size (Mb) | IRRI designation | Country where released | Year of release |
|------------------|-------------------|--------------|------------|--------------------------|------------------|-----------------------|-----------------|
| Swarna           | India             | IR49830      | BC3F2      | 2.3–3.4                  | IR05F102         | India & Bangladesh, Nepal & Myanmar | 2009 2010 2011 |
| IR64             | Philippines       | IR40931      | BC2F2      | 6.5–7.8                  | IR07F102         | Philippines & Indonesia | 2009 |
| Samba Mahsuri    | India             | IR49830      | BC2F2      | 6.5–9.2                  | IR07F101         | Nepal, India          | 2011 2013 |
| TDK1             | Laos              | IR40931      | BC2F2      | 1.5–2.5                  | IR07F1289        | N/A                   | 2010 |
| BR11             | Bangladesh        | IR40931      | BC2F2      | 0.3–2.6                  | IR07F1289        | Bangladesh            | 2010 |
| CR1009           | India             | IR40931      | BC2F3      | 2.7–4.6                  | IR07F1291        | N/A                   | 2010 |
| Ciferang         | Indonesia         | IR64-Sub1    | BC1F2      | 6.5–7.8                  | IR09F436         | Indonesia, Bangladesh | 2012 2013 |
| PSB Rc18         | Philippines       | IR64-Sub1    | BC3F2      | 6.5–7.8                  | IR09F437         | N/A                   | 2013 |

Table 2. Commonly used markers used in development of Sub 1 gene is presented here for reference [30]

| Primer | Sequence | Tm (°C) | Position | Type of marker | Accession | Expected size (bp) |
|--------|----------|---------|----------|----------------|-----------|--------------------|
| RM8300 (SC3)F | GCTAGTGCGAGGTTGACACA | 60 | ~300 kb upstream of SUBIA | SSR | NIp6 | 200 |
| RM8300 (SC3)R | CTCTGCGCGTTCATGGTAT | 60 | | | | |
| GnS2F | CTTCTTGTCTACAACGACACG | 60 | exon of SUBIA | CAPS (Alul/PvuII) | Teqing | 242 |
| GnS2R | TCGATGGGCTCTTGTCTCT | 60 | | | | |
| AEX1F | AGGCAGGAGCTACGATACCA | 62 | non-synonymous SNP for SUBIA | mismatch | 26D17b | No product |
| AEX1R | GCAGAGCGGGTGGCA | 62 | | specific for tolerance | Teqing | No product |
| ART5F | CAGGGAAAGAGATGGTGGA | 60 | SUB1C promoter | 15 bp insertion in NB/93-11 | NB92/93-11 | 217 |
| ART5R | TTGCCCTAGTTGTTTTCAG | 60 | | 118k20a | | 202 |
| Sub1C173F | AACCGCAAAGACACAACCTCC | 60 | exon of SUB1C | 9 bp deletion in NB/93-11 | NB92/93-11 | 164 |
| Sub1C173R | AGGAGGCTGTCCATCAGGT | 60 | | 118k20a | | 173 |

a Nipponbare  
b derived from IR40931-26
3.2 Breeding rice for anaerobic germination

The phenomenon of tolerance to flooding during seed germination, referred to as anaerobic germination (AG), is one of the indispensable characters needed to ensure optimum plant population in direct seeded rice in both rain-fed flood-prone and irrigated ecosystems. QTLs for AG tolerance were found on chromosomes 1, 2, 5, and 7 [15], [30]. The study also revealed promising QTLs in Khao Hlan On, a tolerant donor from Myanmar [1], [30]. The QTL with the largest effect was detected on the long arm of chromosome 9 (qAG-9-2 or AG1), having a logarithm of odds (LOD) score of 20.3 and explaining 33.5% of the variation for this trait. Similarly, on the short arm of chromosome 7 a major QTL was detected (qAG7.1 or AG2), derived from the tolerant donor variety Ma-Zhan Red [30]. The combination of these two big effects QTLs to provide higher tolerance, assuming that the effect of the two QTLs proved to be additive or synergistic.

3.3 Breeding rice for deepwater or stagnant flooding

The major characteristics feature for the survival of deepwater rice is internode elongation under stagnant flooding condition which facilitates the uppermost leaves come protruding the water level and ensures photosynthesis [38], [3], [30]. Several studies have identified QTLs for deepwater traits, such as internode elongation and number of elongated internodes. It was reported that the QTL on chromosome 12 contributed the most rapid internode elongation in deepwater stress conditions [30]. By positional cloning, QTL within the genes: SNORKEL1 (SK1) and SNORKEL2 (SK2) were identified.

4. FUTURE PRIORITY FOR RICE BREEDING

4.1 Breeding rice for Anaerobic germination tolerance

The major QTL AG1 has been successfully introgressed derived from Khao Hlan On (KHO) variety into IR64 and IR64-Sub1 and effort are being made to introgression of this QTL into other genetic backgrounds such as Cihang-Sub1, PSB Rc18-Sub1, and PSB Rc82 and other mega varieties in the subsequent years. Likewise introgression of the major QTL AG2 derived from Ma-Zhan Red into many popular varieties are on prime focus and work has been underway. The major QTLs controlling tolerance of anaerobic germination are scattered throughout the rice genome [1] [30] (Angaji et al. 2010; Septiningsih et al. 2013; unpublished data). QTL pyramiding is an very viable strategy assuming that the effects of the QTSs are additive in nature. Ultimately, these pyramided lines could be used directly as improved varieties.

4.2 Breeding rice for tolerance to stagnant flooding

The genetic control mechanism and physiology of stagnant flooding is still less known. All the efforts are concentrated towards unravelling the genetics of stagnant flooding in the current breeding programs. To achieve the progress, mapping population
development (F2 derived bulks) and selective genotyping to identify QTLs using classical QTL mapping approach to shorten the breeding cycle. A RIL population has been already prepared from IRRI 154 source, a identified variety of stagnant flooding tolerance for QTL mapping. Backcross derived mapping population and association mapping is a most viable tool to combine QTL mapping for development of new breeding lines. So far, new breeding lines have been developed and evaluated by IRRI, Bangladesh and Nepal. The achievement of the breeding program to develop tolerance to stagnant flooding are quite encouraging.

4.3 Sub 1 and Beyond

Pyramiding Sub 1 genes with other biotic and abiotic stress tolerance genes is also research focus of the rice breeding program. Alongwith this considerable works are being done to develop more efficient Sub 1 varieties and Sub 1plus rice varieties to confer additional tolerance to transient flash flooding.

5. CONCLUSION

Tremendous efforts and resources were invested on breeding for submergence tolerance and significant achievements were harvested in the past. Series of submergence tolerance varieties were developed in many countries and contributed to the food security and many popular varieties at respective areas that were susceptible to submergence were improved by introgression of Sub 1 gene. Besides this, several efforts were being done to overcome the other effects of submergence like stagnant flooding and flooding tolerance during germination particularly in the direct-seeded rice in rainfed and irrigated ecosystems. The progress towards the breeding for both of these submergence effects are in desired level and few anaerobic germination regarded as AG lines have been developed introgression with Sub 1 varieties. This will provide the added advantages for the rice varieties. Similarly, Sub 1 varieties are also further improved by providing stagnant flooding tolerance after identification of suitable donors for this environments. To cope with the adverse effect of climate change the submergence tolerant varities are also strived to tolerate other biotic and abiotic stresses by pyramiding the resistance genes of interest to provide added tolerance to every kind of stresses.

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