

Strategies and Current Progress for Submergence Tolerance in Rice: A Review

Anirneeta De, Avishek Dey, Subrata Raha, Dipak Kumar Kar

Received 2 January 2022, Accepted 14 February 2022, Published on 14 December 2022

ABSTRACT

Being a staple food of around half of the population all over the world, especially in South and South-east Asia, rice have always been a highly flood-threatened crop in farmer's field. Identification of the Sub 1 gene that confers tolerance against submergence had a great impact in this context and introgression of the said gene into different high-yielding varieties through crossing has been successful till date. In this review the effort has been made to accumulate the types of floods affecting rice plants, reasons why rice plants get affected, various tolerance mechanisms or strategies of a plant resisting the flood condition, history

of Sub1 gene at molecular level, transfer of the gene into different varieties through MAB, along with other biotic resistance associated with Sub1 gene. Now it is necessary to find other QTLs (Quantitative Trait Loci) imparting tolerance against inundation in addition to Sub1 gene. In this aspect, a new gene i.e., Leaf Gas Film 1 gene might be utilized to enhance submergence tolerance in rice plants by facilitating oxygen and carbon-di-oxide exchange underwater. Search of these kind of genes/QTLs needs constant research to meet the hunger of the growing populace of the world.

Keywords Rice, Submergence tolerance, Sub 1, LGF 1, Review.

INTRODUCTION

Flooding or submergence is undoubtedly one of the most detrimental and the third most hazardous abiotic stress, after heat and drought, which is affecting crop production by causing a huge loss in both seasonal and non-seasonal crops (Oladosu *et al.* 2020). From the climate change scenarios, it can be further predicted that these types of incidences like floods, drought and their intensities might increase in the future especially in the tropics and subtropics (Patz *et al.* 2005). Roughly one and half of the world population, including all of East and Southeast Asia is fully dependent upon rice as a staple food (Encyclopaedia Britannica 2020). At this moment, rice is the most flood-threatened crop of Asia, where about 30% of people living in dire poverty (almost 700 million) dwell in flood-prone rice cultivating regions of South Asia, with India,

Anirneeta De*
Dept. of Botany, Sidho-Kanho-Birsha
University, Purulia 723104, India

Avishek Dey
Asst. Prof., Dept. of Botany, R. C. College, Purulia, India

Subrata Raha
Prof., Dept. of Botany, Sidho-Kanho-Birsha University, Purulia,
India

Dipak Kumar Kar
Vice-Chancellor, Sidho-Kanho-Birsha University, Purulia 723104,
India

Email: anirneeta777@gmail.com

*Corresponding author

Nepal and Bangladesh accounting for half of the above-stated figure (Oladosu *et al.* 2020). In India out of 16.1 million hectares of rice-growing area, 5.2 million are affected by flood (Bailey-Serres *et al.* 2010). The urge to step up the current agricultural yield potential to feed the ever-growing population of the world which is expected to be 9 billion by 2050 still remains a challenge alongside the prediction of higher flooding regime associated with the climate change (Godfray *et al.* 2010).

It's quite evident that due to the world-wide environmental degradation, there has been lots of changes in nature which includes global warming, abrupt change in weather pattern. It causes frequent flood in areas where there was no such incidence of submergence reported earlier. This leads to drastic yield reduction of standing crops in field condition. So, it's necessary to explore and utilize each aspect of research in this field along with its further extensive study to combat this situation. This review accumulates different strategies of plants to stand flooded condition, genes/QTLs related to submergence tolerance found so far, discoveries of other important genes that might contribute to this kind of tolerance, finding co-relation between the major genes with other resistant activities. That is why this review is very much relevant, as it is the need of the hour to buckle up and pursue all the possibilities to fight the disastrous climatic condition in order to stabilize the yield in farmers' field following the lab to land approach.

Flooding stress and its affects on rice plants

The main categories of flood during different growth stages of rice are-

Submergence during germination - Flooding that occurs just after direct seeding in the field, causes Anoxia/Hypoxia. Here the plants need to follow anaerobic germination (Magneschi and Pereta 2009). This leads to low germination, poor growth of seedlings and also seedling death.

Complete/partial submergence during vegetative stage- This is common in river basin areas, and affects the plant at seedling or tillering stage. Plants remain

flooded for days to weeks. Low land rice cultivars commonly face this kind of flooding.

Deepwater flooding- Flood remains constant for a prolonged period of time and the water level ranges from 25-50 cm and may sometimes reach upto 4 m (Oladosu *et al.* 2020) or it may also remain for almost the entire season with a water level of >50cm (Mackill 2006, Kato *et al.* 2014). Mostly found in low land areas i.e. mangrove regions. Floating rice genotypes are adapted to such type of flooding.

Apart from these, there are 'stagnant flood', where the water level remains static for a longer time (few months) occurring mostly in the monsoon period, and 'flash flood' which occur due to sudden heavy rainfalls causing complete/partial submergence and recedes within some days (few weeks). During stagnant flood, rice plants try to increase their stem length by elongating their internodes to avoid submergence and when the water subsides, the plants are often prone to lodging, thereby accounting a major yield loss. But in flash-floods, rice plants try to reserve their nutrients and regain their growth after the flood settles down (Winkel *et al.* 2013).

Plants used to face several biophysical constraints including temperature, pH of soil and water, depth of water, turbidity, duration of the flood, leaf and aerenchymatic cell morphology, gas diffusion ability, intensity of light during flooding which eventually affect the growth, development and yield of the crop. The turbidity of water is caused due to the presence of phytoplankton, organic matter and silt in it which does not allow enough amount of sun light to enter into the water and reach the plant canopy. As a result, the rate of photosynthesis is reduced. Consequently, the amount of oxygen (O₂) and carbon-di-oxide (CO₂) also become limited which further leads to limited respiration i.e., hypoxia and then total absence of oxygen i.e., anoxia. All these factors are detrimental to plant physiology and survival (Sarkar *et al.* 2006). The importance of solar radiation in submerged condition was further explained by an experiment where plants were grown in different conditions i.e., complete submergence (no light) and submergence with some light. The difference between plant growth and survival was prominently better in the submerged

condition with light which ascertained the necessity of light under water (Pucciariello *et al.* 2014).

In rice, deficiency of light and oxygen are connected with the formation of ROS (Reactive Oxygen Species) such as hydrogen peroxide, hydroxyl radical, super oxide anion. These ROS led to the death of plants by severely damaging the cellular configuration. Some rice cultivars are able to detoxify the ROS activities and restore its growth. These cultivars inherit the mechanism of producing natural anti-oxidants i.e., phenols, ascorbate, carotenoids. which reduce the oxidative damage to the plants. These compounds help the cultivars in restoring chlorophyll, regenerate new leaves and sustain their growth (Oladosu *et al.* 2020). Among all the natural anti-oxidants ascorbate was studied and was observed to accumulate in root cells of rice plants during hypoxic condition. Its amount declined when de-submerged (Das *et al.* 2004). Some other studies also state that ROS are formed even when plants are re-aerated after enduring anoxic/hypoxic condition and cause harm to plants (Kirk *et al.* 2014).

It's also mentioned that, during inundation or water-logged condition, different toxic compounds increase in anoxic/hypoxic soils which enter the plant and affect the root and shoot tissues. In fact, upon re-aeration after a period of oxygen deprivation, the amount of ethanol accumulated in the submerged parts of rice plants does not reduce, instead, the entrapped ethanol is converted into acetaldehyde causing post-anoxic cell injuries (Kurokawa *et al.* 2018, Ismail 2018).

Defence strategies of rice plants during submergence

In flooding or submerged condition, the gas exchange underwater is restricted which leads to a deficiency in energy and carbohydrate in plants. Impeded gas exchange leads to rapid accumulation of ethylene in submerged plant organs. Flooded condition increases the expression and activity of the ethylene biosynthetic enzymes i.e., 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase and ACC synthase in several species including rice (Van Der Straeten *et al.* 2001, Lee *et al.* 2011, van Veen *et al.* 2013). Due to these

reasons ethylene is known to be the key regulator of flood adaptive traits. Rice involves the following ethylene-mediated responses.

Escape- In this type of response rice cultivars promote their growth by elongating the internodes to outgrow the flood water level. Very few cultivars, specifically the deepwater rice show this kind of characteristics. The SNORKEL (SK) locus on chromosome 12 is primarily responsible for shoot/internode elongation. The SK locus controlling this quantitative trait, encodes two transcription factors of ethylene-inducible Ethylene Response Factor (ERF): SK1 and SK2. Two other loci on chromosome 1 and 3 along with SK locus can show full escape response (Hattori *et al.* 2008, 2009, 2011). Higher level of ethylene in submerged plant organs increases biosynthesis of Gibberellic acid (GA) which is essential for internodal elongation (Hoffmann- Benning and Kende 1992). Expression of these genes in deepwater rice allows them an elongation by 20-25 cm/day which helps to keep the drowned portion of the plants aerated by restoring the gas exchange with environment. Introgression of these genes in non-deepwater rice triggers internodal elongation, even in no flood situation (Hattori *et al.* 2009).

Quiescence- This is another strategy where rice cultivars try to restrict their energy consumption instead of elongating their height to outgrow the flood water level. They prevent the exhaustion of non-structural carbohydrates (NSC) i.e., their energy reservoir which becomes limited during submergence (Kurokawa *et al.* 2018, Ismail 2018). The low land cultivars show this kind of tolerance activity. A mutation in a transcription factor of the ethylene response factors in the Sub-1 locus on chromosome 9 caused this response (Xu *et al.* 2006). Cultivars having this mutation are fully tolerant to total submergence and can survive in this condition for up to 2 weeks (Fukao *et al.* 2006, Xu *et al.* 2006). This locus encodes three transcription factors, Sub 1A, Sub 1B, Sub 1C. In the cultivars with mutated Sub 1 locus, during submerged condition, causes a massive accumulation of Sub 1A transcripts which reduces ethylene biosynthesis and its responsiveness, thereby limiting the intermodal elongation. Sub 1A also induces mRNA and protein accumulation of two negative regulators of Gibberel-

lic acid (GA) signalling i.e., SLENDER RICE 1 and SLENDER RICE-LIKE 1 blocking the GA regulated growth promoting genes and restoring the energy within the plants. Schimitz *et al.* (2013) mentioned that, SUB1A-1 allele of SUB 1A locus upregulates brassinosteroid (BR) synthesis. Brassinosteroids are known to induce a GA catabolic enzyme named CA2ox7. So, basically in the quiescence stage, plants suppress the shoot elongation and stores NSC, so that after surviving the submerged condition they can revive themselves easily. A comparative diagram of escape and quiescence strategies is in Fig. 1. (Bailey *et al.* 2010, Septiningsih and Mackill 2018).

Aerenchymatous tissues- Ethylene is an important signal triggering the lysigenous aerenchyma formation in rice in flooding-induced condition (Fukao and Bailey-Serres 2008, Sauter 2013). These tissues are formed on both roots and shoots. It helps in aeration of plants through different ways. Aerenchyma tissues connect the flooded parts of the plants with those parts which are still in aerial contact during partial submergence. While in complete submergence, these tissues ease out the access towards available oxygen sources (e.g., gas films on submerged leaves, oxygen

produced in underwater photosynthesis). In anoxic/hypoxic condition these tissues reduce the number of oxygen consuming cells. All these responses help plants in low-level-oxygen-supply condition (Sasidharan and Voesenek 2015). There are two types of aerenchyma tissues- lysigenous (internal gas spaced formed by regulated cortical cell death) and schizogenous (formed due to cell separation during tissue development) (Takahashi *et al.* 2014). Rice cultivars develop lysigenous types of tissues and the aerenchyma formation is augmented during submerged condition (Takahashi *et al.* 2014, Yuki Yoshi and Karahara 2014), though this ethylene dependent aerenchyma formation highly varies in different genotypes (Parlanti *et al.* 2011, Yin *et al.* 2013). In case of shoots, during waterlogged/submerged condition, ACC (1-aminocyclopropane-1-carboxylic acid), precursor of ethylene is transported there (various parts of the shoot) through xylem which triggers the formation of aerenchyma on shoots (Jackson 2002).

Adventitious roots - Another adaptive response of rice plants during flood is the formation of a whole new secondary root system. Rice stems are known to develop adventitious root primordia at each node

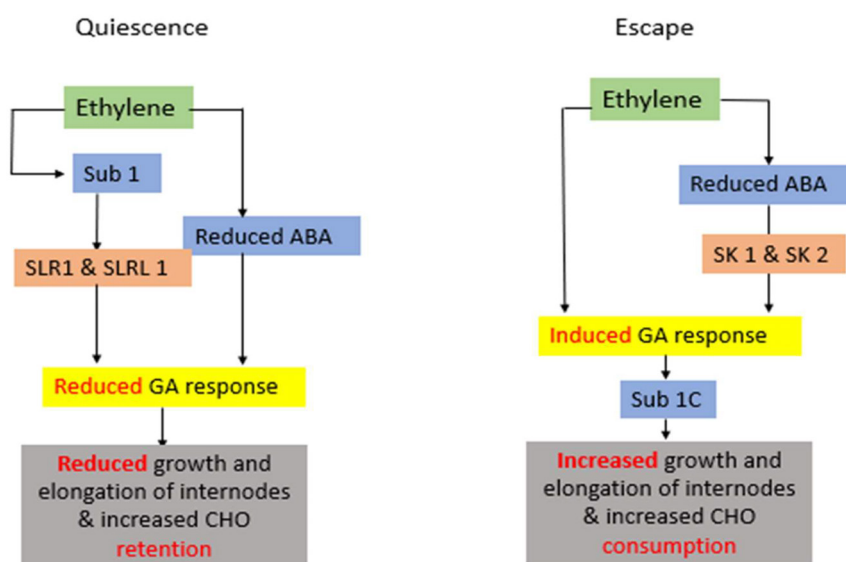


Fig. 1. In 'quiescence' strategy higher ethylene production leads to the expression of Sub1A gene which activates slender rice and slender rice like gene which turns down the elongation process of internodes. Whereas, in 'escape' strategy ethylene induction leads to higher Gibberalic acid production which elongates the internodal elongation and energy consumption.

which grows along with the plant's growth, but the roots emerge only when the plant gets submerged. Here again ethylene plays a pivotal role. Due to lowered oxygen level and gas diffusion rate, ethylene accumulation takes place which gives rise to AR growth (Lin and Sauter 2018, Lorbiecke and Sauter M 1999). Primarily ethylene induces AR growth and epidermal cell death and these two processes are also enhanced by GA (Steffens and Sauter 2005). It has been further revealed that the growing ARs exert a mechanical force on the epidermal cells leading to cell-death. This process also requires ethylene-mediated ROS formation (Steffens *et al.* 2012).

Submergence tolerant rice germplasms

Crops grown in different low land situation are subjected to flooding for various period of time from ages. As wild varieties and landraces have always shown well adaptation against different biotic and abiotic stresses, farmers have thereby planted traditional varieties during submergence which could withstand this kind of water stress (Ahmed *et al.* 2013). In case of rice, few landrace/traditional varieties had the mechanism to survive flooded condition which was recognized in the 1950s. Further screening of this type of landrace was conducted by IRRI in 1970s where two Indian accessions i.e., FR13A and FR43B from Dhalputtia and Bhetnasia of Odisha respectively and some Sri Lankan accessions i.e., Kurkaruppan, Goda Heenati, Thavalu were found to be highly submergence tolerant. FR13A was found to be 100% tolerant for 7 days of complete submergence of 10 days old seedlings (Mackill *et al.* 1996, HilleRisLambers and Vergara 1982, Vergara and Mazaredo 1975) while the Sri Lankan accessions showed 75% survival rate after seven days submergence of 10-day-old seedlings (Vergara and Mazaredo 1975). Some other accessions were also screened from Bangladesh, Cambodia, China, Myanmar and other countries (Ahmed *et al.* 2013, Oladosu *et al.* 2020). During germination Ma-Zhan Red, Nanhi, Khao Hlan On and Khaiyan landraces were submergence tolerant. Leuang Pratew 123 and Khao Tah Haeng 17 are capable of tolerating both stagnant floods of up to 80 cm and flash floods during their early vegetative stage (Oladosu *et al.* 2020). These lines, during total submergence, had the ability to block ethylene production, preserve the

chlorophylls on the leaves, detain shoot elongation, reserve carbohydrates, form aerenchyma tissues as well as adventitious roots and thereby outlive this situation (Ella *et al.* 2003). Further researches with these lines were conducted and FR13A was found to be the most tolerant line against submergence in different environments and seasons. The initials 'FR' of FR13A came from the word 'Flood-Resistant' as it was reported that India scientists had previously found these varieties to be flood-resistant (Vergara *et al.* 1976). But these lines were very low yielding (2t/ha) than the semi-dwarf commercial varieties (6-8 t/ha) and also had other disadvantages like photosensitivity, poor grain quality, taller stature. So, these varieties, mostly FR13A were used as the donor parent in different breeding programs to develop high yielding submergence tolerant lines.

Qtl's associated with submergence tolerance in rice

The landmark in the history of breeding for submergence tolerant lines in rice is the discovery of the QTL controlling the submergence i.e., SUBMERGENCE 1 or SUB 1 locus. Physical mapping identified this locus on the long arm of Chromosome 9 of rice genome near the centromere and this Sub 1 gene was found to be responsible for 70% of the phenotypic expression (Xu and Mackill 1996) whereas the remaining 30% variation was due to some minor QTLs (Nandi *et al.* 1997, Toojinda *et al.* 2003). Xu *et al.* (2006) performed a fine mapping of Sub 1 QTL and narrowed its location within 0.06 cM from a mapping population of a cross between IR40931-26 (submergence tolerant indica variety) and M-202 (submergence intolerant japonica variety) [IR40931-26 is a derivative of FR13A]. Physical mapping of SUB1 locus was carried out by analyzing five BAC contigs from the intolerant indica varieties (Teqing) and the contigs of thirteen binary clones of IR40931-26. This confined the Sub1 region within the markers CR25K and SSR1A spanning for a length of 182 kb. As this region is nearer to the centromere, it was considered as one of the reasons of suppressed recombination in this segment. It showed 10.7-fold lower recombination rate as compared to the whole genome (Xu *et al.* 2006). Sub1 region contains three genes encoding ERF DNA binding protein domains i.e., Sub1A, Sub1B and Sub1C. Physical mapping in

another submergence intolerant japonica variety, Nipponbare showed a genetic rearrangement. It lacked the Sub1A gene but encoded both Sub1B and Sub1C genes (GenBank AP006758 and AP005705) with 142kb of a total length of its corresponding region (Xu *et al.* 2006). In FR13A the expression of both Sub1A and 1C mRNA were strong but lasted for a limited phase during submergence and also reduced when de-submerged whereas Sub1B transcripts increased slightly which indicates that Sub1A is the most crucial gene associated with submergence tolerance. In a survey of Sub1 locus haplotypes in 21 (4 japonica and 17 indica) accessions by Xu *et al.* (2006) showed that Sub1A had two, Sub1B had nine and Sub1C had seven alleles. The two alleles of Sub1A are Sub 1A-1 and Sub 1A-2. These two alleles are identical except for the presence of an amino acid, i.e., Sub1A-1 has Ser186 whereas Sub1A-2 has Pro186. Sub1A-1 is responsible for the tolerance trait and was found in FR13A also. During the stress condition Sub1A-1 allele promotes rapid accumulation of transcripts in leaves of 14-28 days old plants; whereas the expression of Sub1A-2 allele is way lower (Fukao *et al.* 2006, Xu *et al.* 2006). It was also found from the survey that few indica and aus varieties encoded the Sub1A gene whereas all the subspecies carried the Sub1B and Sub1C gene (Bailey-Serres *et al.* 2010, Xu *et al.* 2006). From the Nipponbare transgenics, the Sub1A promoter was found to control GUS activity in the leaves during submergence, suggesting

that Sub1A gene might also be responsible for cell division/elongation in leaves under submergence (Bailey-Serres *et al.* 2010). Sub1A gene also accumulated in variable levels of transcripts in the nodes and internodes at heading stage (Singh *et al.* 2010). A table (Table 1) mentioning different lines having various tolerant alleles of the above said Sub 1 gene from different studies is given below.

Recent progress in breeding of submergence tolerant lines

As mentioned earlier, the first report of flood tolerance rice genotypes was in 1950. Then in the 1970s the proper screening by IRRI involved the discovery of FR13A, FR43B, Goda Heenati, Thavalu along with some other accessions where FR13A stood out in performance (Vergara and Mazaredo 1975). In 1990s the FR13A derivative IR49830-7-1-2-2 was developed and further attempts were made to introduce the submergence tolerant in short to medium statured lines (Oladosu *et al.* 2020, Mishra *et al.* 1996). IRRI carried out a series of crossing programs with the submergence tolerant landraces but poor grain quality, photosensitivity, lesser yield inherited from the parent landraces limited this development program (Oladosu *et al.* 2020).

After the discovery of SUB 1 QTL, MAB or Marker Assisted Backcrossing helped in the incorporation of the gene in particular, into widely adapted farmers' varieties (Bailey-Serres *et al.* 2010, Xu *et al.* 2004). Some high-yielding varieties where SUB 1 gene has been introgressed are Swarna, Samba Mahsuri, IR64, BR11, CR1009 and Thadokkam 1 (Septiningsih *et al.* 2009). Swarna Sub 1 was the earliest example of submergence tolerant mega-variety where the gene was incorporated through MAB in an Indian HYV, Swarna within a two-year work frame. Both the varieties (Swarna and Swarna Sub 1) showed no significant difference in grain yield and quality in non-submerged condition (Sarkar *et al.* 2006, Neeraja *et al.* 2007, Septiningsih *et al.* 2009), whereas, in inundated condition for >10 days Swarna Sub 1 showed >2-fold higher yield as compared to Swarna (Septiningsih *et al.* 2009). Samba Mahsuri Sub 1 and IR 64 Sub 1 were also derived by repeated backcrossing followed by self-pollination. In each of the cases

Table 1. Some genotypes are shown where the presence of Sub1A, 1B and 1C genes and their alleles are stated.

Line or cultivar	Sub1A allele	Sub1B allele	Sub1C allele	Reference
FR43B	A ₁	-	C ₁	Xu <i>et al.</i> (2006),
Goda Heenati	A ₁	B ₆	C ₁	
Heenkarayal	A ₁	-	C ₁	Singh <i>et al.</i> (2010)
Hindik Wee	A ₁	-	C ₁	
IR40931-33-1-3-2	A ₁	-	C ₁	
IR64-Sub1	A ₁	-	C ₁	
IR8419422-139	A ₁	-	C ₁	
Kaharamana	A ₁	-	C ₁	
Kurkaruppan	A ₁	B ₃	C ₁	
MTU 1	A ₁	-	C ₁	
Swarna Sub 1	A ₁	-	C ₁	
FR13A	A ₁	B ₁	C ₁	
IR40931-26	A ₁	B ₁	C ₁	
DX18-121	A ₁	B ₁	C ₁	
IR48930	A ₁	B ₁	C ₁	

the MAB strategy was to use closely flanked markers to reduce the size of the target introgression, and use of background markers to identify the recurrent parent alleles (Collard and Mackill 2008, Septiningsih *et al.* 2009). Comparative analysis for yield and other agronomic factors was done in submerged and non-submerged condition for all the developed varieties which revealed that SUB1 introgression does not adversely or negatively affect the agronomical performances of the varieties (Sarkar *et al.* 2006, Bailey-Serres *et al.* 2010). FR13A derivative IR49830-7-1-2-2 failed in field performance as it retained many alleles from the non-recurrent parents which lowered its overall agronomic performance (Mackill 2006) but these Sub 1 lines produced through MAB was successful because they retained maximum alleles from the recurrent parents (Oladosu *et al.* 2020, Singh *et al.* 2009). Based on preliminary tests, the observed data revealed that IR64-Sub1, TDK1-Sub1, CR1009-Sub 1 have almost same level of submergence tolerance as compared to Swarna Sub1; tolerance level of BR11-Sub1 was slightly lower whereas Samba Mahsuri Sub1 was the least tolerant among all (Septiningsih *et al.*, 2009). Swarna-Sub1 was released in India, Indonesia, and Bangladesh in 2009-10; BR11-Sub1 and IR64-Sub1 were released in Bangladesh and Philippines and Indonesia respectively (Bailey-Serres *et al.* 2010).

All these newly developed varieties having Sub 1A gene follow the quiescence strategy where they are protected from the submerged condition by accumulating NSCs and other substances that help them to continue gas exchange and underwater photosynthesis (Ismail 2018). As compared to FR13A, the Sub 1 varieties accumulate less NSC which suggests that these varieties are more dependent on the underwater photosynthesis for their survival in submerged condition (Singh *et al.* 2014). Clearly some additional traits can definitely boost up the submergence tolerance of these varieties. In several studies by Winkel *et al.* 2013, Kurokawa *et al.* 2018 it has been proved that gas films facilitate oxygen and carbon-di-oxide exchange underwater. The remarkable discovery of the gene, Leaf Gas Film 1 (LGF1/OsHDS1) by Kurokawa *et al.* (2018) have showed us a new path for further research that will enhance submergence tolerance in rice in another tangent. Though discovery of stronger alleles responsible for longer retention of the volume

of the gas films are still pending (Ismail 2018).

Role of Sub 1 against some biotic diseases of rice

In a study by Chaudhary *et al.* (2015), the submergence tolerant rice lines were found to show reduced infestation of Blast disease (*c.o. Magnaporthe oryzae*). The area under disease progress curve (AUDPC) was measured for leaf blast for Swarna, Swarna Sub 1, Samba Mahsuri and Samba Mahsuri-Sub 1 varieties and Swarna Sub 1 showed least infestation in both submerged and non-submerged condition. The duration of submergence had positive effect on reducing leaf blast in the seedbed condition. Ultimately this study demonstrated that when Sub1 rice genotypes were subjected to submergence for 3-7 days at the seedling stage, the stress conferred tolerance to both submergence and resistance to leaf blast. As Swarna Sub 1 performed the best, it was concluded that Swarna Sub 1 can be promoted in flash-flood effected and blast-prone areas.

Another major threat to rice, Bacterial Leaf Blight (BLB, *c.o. Xanthomonas oryzae pv oryzae*) hinders the production greatly. In terai regions of Nepal, BLB accompanied with flash floods in rice growing fields, cause severe crop loss for both traditional and improved rice varieties. In a study with submergent tolerant and non-tolerant lines, it was observed that the disease was significantly lower on plants transplanted after three to seven day submerged seedlings and the lowest BLB was recorded on rice plants transplanted with seven day submerged seedlings. In this case also Swarna Sub1 had the lowest AUDPC value for BLB with or without the use of submerged seedlings for transplanting and the variety produced the highest grain yield (Chaudhary *et al.* 2015). Flooding can induce disease resistance has also been proved in plants like *Arabidopsis* (Hsu *et al.* 2013).

CONCLUSION

Different mechanisms followed under submerged conditions for survival consists of anaerobic germination, quiescence and escape strategy, production of adventitious roots. Further research can be done to discover some other strategies and utilize them as

well. Definitely discovery of Sub 1 gene is a landmark in submergence breeding, but it is important to find other genes or QTLs that confer tolerance against flooding. Leaf Gas Film 1 gene can be utilized to enhance this tolerance in rice plants. Marker assisted breeding may be non-efficient when multiple and complex characters are taken into account. That is why modern technologies should be utilized in breeding programs. As rice is the staple food in India as well as Asia, subsequent improvement in submergence tolerance and its combining traits, more particularly disease resistance is in urgent need to meet the hunger crisis of our overgrowing population.

REFERENCES

- Ahmed F, Rafii MY, Ismail MR, Juraimi A, Rahim HA, Asfaliza R, Latif MA (2013) Waterlogging tolerance of crops: Breeding, mechanism of tolerance, molecular approaches, and future prospects. *Bio Med Res Int Article ID 963525*, <https://doi.org/10.1155/2013/963525>. [Google Scholar]
- Bailey-Serres J, Fukao T, Ronald PC, Ismail AM, Heuer S, Mackill D (2010) Submergence tolerant rice: SUB1's journey from landrace to modern cultivar. *Rice* 3: 138–147.
- Chaudhary B, Shrestha SM, Singh US, Manandhar HK, Zaidi NW, Thapa RB (2015) Submergence MEDIATES Leaf Blast Resistance in Sub1 and Non-Sub1 Rice Genotypes. *Glb Jrl of Bio, Ag Hlth Sci* 4(1):231-237.
- Chaudhary B, Shrestha SM, Singh US, Manandhar HK, Zaidi NW, Thapa RB, Dangal NK (2015) Evaluation of Sub1 and Non-Sub1 Rice for Resistance to Bacterial Blight Using Submerged and Non-submerged Seedlings. *Agric Biol Sci J* 1(6): 229-234 [<http://www.aiscience.org/journal/absj>]
- Collard BC, Mackill DJ (2008) Marker-assisted selection: An approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society of London B Biological Sciences*. 363:557–572. [Google Scholar]
- Mackill DJ, Coffman WR, Garrity DP (1996) Rainfed Lowland Rice Improvement, International Rice Research Institute, Los Banos, Philippines.
- Das KK, Panda D, Nagaraju M, Sharma SG, Sarkar RK (2004) Antioxidant enzymes and aldehyde releasing capacity of rice cultivars (*Oryza sativa* L.) as determinants of anaerobic seedling establishment capacity. *Bulg J Pl Physiol* 30: 34–44. [Google Scholar]
- Ella E, Kawano N, Yamauchi Y, Tanaka K, Ismail AM (2003) Blocking ethylene perception enhances flooding tolerance in rice seedlings. *Funct Pl Biol* 30: 813–819. [Google Scholar]
- Encyclopaedia Britannica, May 29, 2020
- Fukao T, Bailey-Serres J (2008) Ethylene - A key regulator of submergence responses in rice. *Pl Sci* 175: 43–51.
- Fukao T, Xu K, Ronald PC, Bailey-Serres J (2006) A variable cluster of ethylene response factor-like genes regulates metabolic and developmental acclimation responses to submergence in rice. *Pl Cell* 18: 2021–2034.
- Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Toulmin C (2010) Food security: The challenge of feeding 9 billion people. *Sci* 327: 812–818.
- Hattori Y, Nagai K, Ashikari M (2011) Rice growth adapting to deepwater. *Curr Opin Pl Biol* 14: 100–105.
- Hattori Y, Nagai K, Furukawa S, Song XJ, Kawano R, Sakakibara H, Wu J, Matsumoto T, Yoshimura A, Kitano H *et al.* (2009) The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. *Nature* 460: 1026–1030.
- Hattori Y, Nagai K, Mori H, Kitano H, Matsuoka M, Ashikari M (2008) Mapping of three QTLs that regulate internode elongation in deepwater rice. *Breed Sci* 58: 39–46.
- HilleRisLambers D, Vergara BS (1982) Summary Results of an International Collaboration on Screening Methods for Flood Tolerance; International Rice Research Institute: Los Baños, Philippines, pp 347–353. [Google Scholar]
- Hoffmann-Benning S, Kende H (1992) On the role of abscisic acid and gibberellin in the regulation of growth in rice. *Pl Physiol* 99: 1156–1161.
- Hsu FC, Chou MY, Chou SJ, Li YR, Peng HP, Shih MC (2013) Submergence confers immunity mediated by the WRKY 22 transcription factor in Arabidopsis. *The Plant Cell* doi:10.1105/tpc.113.114447.
- Ismail AM (2018) Submergence tolerance in rice: Resolving a pervasive quandary: A commentary on Kurokawa *et al.* *New Phytologist* 218: 1298–1300.
- Ismail AM, Commentary on Kurokawa *et al.* (2018) *New Phytologist* 218: 1558-1569.
- Jackson MB (2002) Long-distance signalling from roots to shoots assessed: The flooding story. *J Exp Bot* 53: 175–181.
- Kato Y, Collard B, Setininsih E, Ismail A (2014) Physiological analyses of traits associated with tolerance of long-term partial submergence in rice. *AoB PLANTS*. 2014. 6. <https://doi.org/10.1093/aobpla/plu058>
- Kirk GJD, Greenway H, Atwell BJ, Ismail AM, Colmer TD (2014) Adaptation of rice to flooded soils. *Prog Bot* 75: 215–253.
- Kurokawa Y, Nagai K, Huan PD, Shimazaki K, Qu H, Mori Y, Toda Y, Kuroha T, Hayashi N, Aiga S *et al.* (2018) Rice leaf hydrophobicity and gas films are conferred by a wax synthesis gene (LGF1) and contribute to flood tolerance. *New Phytologist* 218: 1558–1569.
- Lee SC, Mustrup A, Sasidharan R, Vashisht D, Pedersen O, Oosumi T, Voeselek LACJ, Bailey-Serres J (2011) Molecular characterization of the submergence response of the *Arabidopsis thaliana* ecotype Columbia. *New Phytol* 190: 457–471.
- Lin C, Sauter M (2018) Control of adventitious root architecture in rice by darkness, light and gravity. *Pl Physiol* 176(2): 1352–1364.
- Lorbiecke R, Sauter M (1999) Adventitious root growth and cell-cycle induction in deepwater rice. *Pl Physiol* 119: 21–30. [Google Scholar]
- Mackill DJ (2006) Breeding for resistance to abiotic stresses in rice: The value of quantitative trait loci. In: Lamkey KR, Lee M, Eds., *Plant Breeding: The Arnel R. Hallauer International Symposium*. Blackwell Publication: Ames, IA, USA, pp 201–212. [Google Scholar]

- Magneschi L, Pereta P (2009) Rice germination and seedling growth in the absence of oxygen. *Ann Bot* 103(2): 181–196. doi: 10.1093/aob/mcn121
- Mishra SB, Senadhira D, Manigbas NL (1996) Genetics of submergence tolerance in rice (*Oryza sativa* L.). *Field Crops Res* 46: 177–181. [Google Scholar]
- Oladosu Y, Rafii MY, Arolo F, Chukwu SC, Muhammad I, Kareem I, Salisu MA, Arolo IW (2020) Submergence Tolerance in Rice: Review of Mechanism, Breeding and Future Prospects. *Sustainability* 12(4): 1632, <https://doi.org/10.3390/su12041632>
- Parlanti S, Kudahettige NP, Lombardi L, Mensuali-Sodi A, Alpi A, Perata P, Pucciariello C (2011) Distinct mechanisms for aerenchyma formation in leaf sheaths of rice genotypes displaying a quiescence or escape strategy for flooding tolerance. *Ann Bot (Lond)* 107: 1335–1343.
- Patz JA, Campbell-Lendrum D, Holloway T, Foley JA (2005) Impact of regional climate change on human health. *Nature* 438: 310–317.
- Pucciariello C, Voeselek LA, Perata P, Sasidharan R (2014) Plant responses to flooding. *Front Pl Sci* 5: 226. [Google Scholar]
- Sarkar RK, Reddy JN, Sharma SG, Ismail AM (2006) Physiological basis of submergence tolerance in rice and implications for crop improvement. *Curr Sci* 91: 899–906. [Google Scholar]
- Sasidharan R, Voeselek L (2015) Ethylene-mediated acclimations to flooding stress. *Plant Physiol* 169(1): 3–12.
- Sauter M (2013) Root responses to flooding. *Curr Opin Pl Biol* 16: 282–286.
- Schmitz AJ, Folsom JJ, Jikamaru Y, Ronald P, Walia H (2013) SUB1A mediated submergence tolerance response in rice involves differential regulation of the brassinosteroid pathway. *New Phytologist* 198: 1060–1070.
- Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S, Ismail AM, Mackill DJ (2009) Development of submergence tolerant rice cultivars: The Sub1 locus and beyond. *Ann Bot* 103: 151–160.
- Septiningsih EM, Mackill DJ (2018) Genetics and breeding of flooding tolerance in rice. In *Rice genomics, genetics and breeding*. Springer, Singapore, pp 275–295.
- Singh N, Dang T, Vergara G, Pandey D, Sanchez D, Neeraja C, Septiningsih E, Mendioro M, Tecson-Mendoza R, Ismail A, Mackill DJ, Heuer S (2010) Molecular marker survey and expression analyses of the rice submergence-tolerance genes SUB1A and SUB1C. *Theor Appl Genet* 121(8): 1441–1453. doi:10.1007/s00122-010-1400-z.
- Singh S, Mackill DJ, Ismail AM (2014) Physiological bases of tolerance to complete submergence in rice involve other genetic factors in addition to SUB1. *Annals of Botany* 6: plu060. doi: 10.1093/aobpla/plu060
- Singh S, Mackill DJ, Ismail AM (2009) Responses of Sub1 rice introgression lines to submergence in the field: Yield and grain quality. *Field Crops Res* 113: 12–23. [Google Scholar]
- Steffens B, Kovalev A, Gorb SN, Sauter M (2012) Emerging roots alter epidermal cell fate through mechanical and reactive oxygen species signaling. *Pl Cell* 24: 3296–3306.
- Steffens B, Sauter M (2005) Epidermal cell death in rice is regulated by ethylene, gibberellin, and abscisic acid. *Pl Physiol* 139: 713–721.
- Takahashi H, Yamauchi T, Colmer T, Nakazono M (2014) In: van Dongen JT, Licausi F, eds. *Aerenchyma Formation in Plants*, Vol 21. Springer, Vienna, pp 247–265.
- Van Der Straeten D, Zhou Z, Prinsen E, Van Onckelen HA, Van Montagu MC (2001) A comparative molecular-physiological study of submergence response in lowland and deepwater rice. *Pl Physiol* 125: 955–968.
- van Veen H, Mustroph A, Barding GA, Vergeer-van Eijk M, Welschen- Evertman RAM, Pedersen O, Visser EJW, Larive CK, Pierik R, Bailey- Serres J *et al.* (2013) Two *Rumex* species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. *Pl Cell* 25: 4691–4707.
- Vergara BS, Jackson B, De Datta SK (1976) Deep Water Rice and its Response to Deep Water Stress. *Climate and Rice*, International Rice Research Institute: Los Banos, Philippines, pp 301–319. [Google Scholar]
- Vergara BS, Mazaredo A (1975) Screening for Resistance to Submergence under Greenhouse Conditions; Bangladesh International Rice Research Institute: Dhaka, Bangladesh, pp 67–70. [Google Scholar]
- Winkel A, Colmer TD, Ismail AM, Pedersen O (2013) Internal aeration of paddy field rice (*Oryza sativa*) during complete submergence—importance of light and floodwater O₂. *New Phytol* 197: 1193–1203. [Google Scholar]
- Xu K N, Deb R, Mackill DJ (2004) A microsatellite marker and a codominant PCR-based marker for marker-assisted selection of submergence tolerance in rice. *Crop Sci* 44: 248–253.
- Xu K, Mackill DJ (1996) A major locus for submergence tolerance mapped on rice chromosome 9. *Mol Breed* 2: 219–224.
- Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, Ismail AM, Bailey-Serres J, Ronald PC, Mackill DJ (2006) SUB1A is an ethylene-response factor-like gene that confers submergence tolerance to rice. *Nature* 442: 705–708.
- Yin D, Chen S, Chen F, Jiang J (2013) Ethylene promotes induction of aerenchyma formation and ethanolic fermentation in waterlogged roots of *Dendranthema* spp. *Mol Biol Rep* 40: 4581–4590
- Yukiyoshi K, Karahara I (2014) Role of ethylene signalling in the formation of constitutive aerenchyma in primary roots of rice. *AoB Pl* 6: plu043.