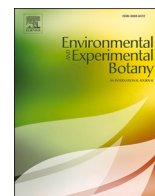




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Review

Submergence stress in rice: Adaptive mechanisms, coping strategies and future research needs

Anjani Kumar, A.K. Nayak*, P.S. Hanjagi, Kavita Kumari, Vijayakumar S, Sangita Mohanty, Rahul Tripathi, P. Panneerselvam

Crop Production Division, ICAR – National Rice Research Institute, Cuttack, Odisha, 753 006, India



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ABSTRACT

Rice is a crop of primary importance in regions, where two-thirds of the world's starving population reside. Recent climate change projections anticipate spatial shift in precipitation pattern and increase of flooding events that may have negative effects on rice yield and economic returns. Efforts for increasing rice production in areas prone to submergence stress will directly benefit hundreds of millions of people dependent on rice as their staple food. This necessitates an objective review of physiological mechanisms and management practices, which could sustain crop productivity under partial or complete submergence. Submergence usually reduces photosynthesis rate that results in quick depletion of the carbohydrate reserve and ultimately the plant dies. Varieties introgressed with *SUB1A* QTL maintains higher activity of alcohol dehydrogenase and low rate of chlorophyll degradation and thus exhibits better survival under submergence. Prolonged submergence results in a significant reduction in soil redox potential and the heavy influx of flood water promotes runoff, volatilization and deep percolation which leads to loss of sizeable amount of nutrients and ultimately causes nutrient deficiency in soil. Thus, to ensure optimum yield, it is essential to alter the nutrient schedule when plant is subjected to submergence stress. Agronomic management practices like seed priming, higher seed rates, alteration in crop geometry and other improved seeding methods enhance production efficiency by boosting germination, early growth and optimum partitioning of photosynthates to vegetative and reproductive parts. This review critically explores the complex problems faced by rice crop during submergence, physiological mechanisms that helps plant to cope up the submergence stress, as well as available cost-effective management strategies to arrest the yield decline.

1. Introduction

Submergence stress affects over 22 million ha rice area (Sarkar et al., 2006) and cause an annual yield loss of over 600 million to 1 billion US\$ annually in Asian countries (Dey and Upadhaya, 1996; Herdt, 1991). This issue is likely to get aggravated, as the flood affected areas are anticipated to increase substantially in the era of global warming (Coumou and Rahmstorf, 2012; IPCC, 2007).

Generally, two types of flooding affect rice, one is flash flooding (rapid rise of water levels with submergence of crop for 1–2 weeks) and another is stagnant flooding where water level exceeds 100 cm depth and remains stagnant at these depths for several weeks. The semi-aquatic nature of rice plant makes it capable of growing under water-logged and/or submerged condition for a considerable period. This is possible due to elongation of submerged shoot organs at faster rates by

developing aerenchyma, that allow sufficient internal transport of oxygen to submerged plant parts from the re-emerged elongated shoot (Jackson and Ram, 2003; Magneschi and Perata, 2009). The process of energy generation and detoxification of fermented products through coleoptile elongation lead to survival under the conditions of low oxygen (Miro et al., 2017). The germination and early seedling growth stage of rice has been found to be highly intolerant to submergence (Ismail et al., 2009; Angaji et al., 2010; Joshi et al., 2013). Apart from germination, submergence also brings many morphological and physiological changes in rice plant. During submergence, rice plant survives by elongation of leaf sheath and blade at seedling stage and internodes at vegetative growth stage (Haque, 1974). If the flooding duration exceeds 2–3 weeks, even the submergence tolerant varieties try to expose their leaf tip above the water surface for ensuring survival (Sarkar and Bhattacharjee, 2011; Colmer et al., 2014). Since this elongation process

* Corresponding author.

E-mail addresses: anjaniias@gmail.com (A. Kumar), aknayak20@yahoo.com (A.K. Nayak), psh7160@gmail.com (P.S. Hanjagi), kavita.iari.9@gmail.com (K. Kumari), vijitnau@gmail.com (V. S), sangitamoha@gmail.com (S. Mohanty), rahulcrri@gmail.com (R. Tripathi).

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is an energy extensive process, which curtails the availability of energy required for post submergence plant growth, and thus it adversely affects the post submergence survival (Singh et al., 2001; Das et al., 2005). The presence of turbid water or luxuriant algal growth on water surface hinders the light transmission through the floodwater, which results in decrease in photosynthesis (Setter et al., 1995; Bhaduri et al., 2020). The submerged plants maintains its metabolism by utilizing the reserve carbohydrate and due to slow photosynthesis rate the reserve is exhausted very soon and ultimately the plant dies (Sarkar and Panda, 2009; Luo et al., 2014). The ability of a variety to tolerate submergence depends on the amount of carbohydrate present in plant parts (Emes et al., 1988; Chaturvedi et al., 1995; Mallik et al., 1995). The restricted shoot elongation in submergence-tolerant rice varieties helps to conserve carbohydrate reserves which is helpful in restarting the development process upon de-submergence (Ismail et al., 2009; Kawano et al., 2009). Thus, post flood availability of carbohydrate is important for recovery from submergence shock (Chaturvedi et al., 1996; Singh et al., 2001; Ram et al., 2002). Since, tolerant landrace seedlings have the ability to conserve about 30–50 % more non-structural carbohydrate (NSC) as compared to sensitive genotypes, hence their post flood recovery rate is faster (Chaturvedi et al., 1996; Sarkar, 1998). Three hormones namely ethylene, abscisic acid (ABA) and gibberellins (GA) are responsible for changes in internode elongation during flooding (Kende et al., 1998; Van Der Straeten et al., 2001; Vriezen et al., 2003). Due to enhanced synthesis and entrapment of ethylene under submerged conditions, the underwater leaf senescence is accelerated (Singh et al., 2014). Presence of hydrophobic wax on rice leaves creates a gas film, which helps with respiration and photosynthesis under submergence. Leaf Gas Film (LGF) reduced *in planta* accumulation of ethylene due to its better dissipation during submergence, thereby delaying the process of ethylene induced leaf senescence under submergence (Chakraborty et al., 2020).

Numerous novel agronomic approaches can be deployed to enhance rice tolerance for submergence like selection of suitable rice variety, higher seed rate, seed priming, optimum sowing depth, seedling age, wider spacing, pre & post nutrient/amendments application and application of certain growth regulators (Munda et al., 2016; Bishoyi et al., 2017). Anaerobic germination (AG) tolerant genotypes of rice could overcome the problem of crop establishment (under flooded/ submerged condition) under direct seeded rice (DSR) conditions (Ismail et al., 2009; Miro et al., 2017; Chamara et al., 2018; Lal et al., 2018; Kumar et al., 2016a,b). Further, *SUB1* introgressed varieties can tolerate 10–18 days of complete submergence, thus submergence & AG intolerant lines can be considered ideal for submerged conditions (Lal et al., 2018). Submergence causes poor rice seedling establishment, which can be compensated with optimum or higher seed rate in DSR (Sharma and Ghosh, 1998; Lal et al., 2018; Illangakoon et al., 2018) and higher seedlings m^{-2} in transplanted rice (Reddy et al., 1990). Seed priming and seed coating materials also help to prolong viability of seeds under submergence (Ella et al., 2010; Serna-Saldivar, 2010; Mora et al., 2013; Chamara et al., 2018). In similar context, fresh and viable seeds were found to be more useful; as flooding decreases the activities of superoxide dismutase (SOD) & catalase, however, it increases lipid peroxidation in older seeds (Ella et al., 2010). Since, older seedlings are taller, sturdier, and healthier with more mature tissues and high carbohydrate storage and hence are more tolerant to submergence and water-logging (Singh et al., 2005; Ram et al., 2009; Bhowmick et al., 2014; Gautam et al., 2017). Planting depth of more than 1 cm and beyond led to anoxic condition due to sharp decrease in redox potential whereas too much shallow sowing (0.5 cm) leads to floating of developing young seedlings above the water surface and ultimately leads to poor crop establishment (Vartapetian and Jackson, 1997; Magneschi and Perata, 2009; Miro and Ismail, 2013; Chamara et al., 2018). Wider spacing ensures higher underwater radiation, which leads to higher photosynthesis and less senescence and thus it imparts higher post submergence recovery as compared to closer spacing (Bhaduri et al., 2020).

Rice soils undergo many physical and chemical changes during submergence. Besides changes in soil properties, one of the most limiting environmental factor under submergence is the slow diffusion of important gases like oxygen and carbon dioxide (Armstrong, 1979). Similarly, there is a significant change in the redox potential, which varies from +400 mv (near the surface of a flooded soil), to –300 mv (at about 1 cm sub-surface soil). Beyond this depth, a sharp decline of oxygen creates highly anaerobic or anoxic condition that not only affects nutrient availability but also causes accumulation of some phytotoxic compounds (Armstrong and Drew, 2002; Pezeshki and De Laune, 2012). The change in nutrient dynamics (Kumar et al., 2019) under submerged condition makes it compulsory to alter the nutrient schedule so that the submerged plant can recover from the stress quickly and optimum yield can be ensured. Innovative nutrient management practices like application of N (post-submergence) and basal P enhanced NSC content, survival percentage and reduced shoot elongation, which could increase plant survival and productivity under submergence (Gautam et al., 2014; Htwe et al., 2019; Mamun et al., 2017).

Considering the global significance of rice in safeguarding the global food as well as nutritional security, it is imperative to gather information on the agronomic and physiological responses of rice when exposed to submergence stress. In this review, we attempted to summarize the available research results on physiological mechanism of submergence tolerance and effectiveness of various management strategies for enhancing resilience to submergence stress. Thus, the present review will help in understanding the fundamental mechanism of submergence tolerance, new research insights of innovative management practices for mitigating submergence stress.

2. Physiological mechanisms of submergence tolerance in rice

Rice owing to its semi-aquatic nature deploys several physiological and biochemical mechanisms that enables it to adapt to different kinds of flooding stresses. Submergence tolerance being an intricate trait, is attributed to several physiological or agronomic characteristics. To cope up the oxygen shortage states (hypoxic or anoxic) arising due to submergence, plant deploys stage specific tolerance/adaptation mechanism.

2.1. Germination stage submergence tolerance mechanisms (metabolic and escape strategy)

Due to the reduced production costs and mechanization in the last decade, farmers are adopting wet and dry direct seeding in rain-fed and irrigated fields in Asia (Kumar and Ladha, 2011). However, because of heavy rainfall, uneven soil leveling, or poor drainage, these areas experience flooded conditions post sowing. When rice plants encounter this flooding stress during germination, the plant tissues are exposed to oxygen deficiency. As a response to the flooding, metabolic and molecular responses are reprogrammed to withstand anaerobic conditions (Dwivedi et al., 2018). Rice plant has evolved various survival strategies (Metabolic adaptation and/or escape) under hypoxia (low O_2) or anoxia (zero O_2) (Lee et al., 2009; Ma et al., 2020; Loreti and Striker, 2020) for tolerance to submergence (Fig. 1).

Due to relatively low amount of ATP produced under anaerobic conditions, anaerobic germination (AG) is a highly challenging process. Tolerant rice genotypes display fast germination and coleoptile elongation, anaerobic metabolism is enhanced by efficient starch-to sugars hydrolysis, and rapid emergence above the water surface (Lee et al., 2009). It has been observed that tolerant and susceptible rice genotypes show differences in their physiology and gene expression. Early (12–24 hours after seed imbibition) increase in the activity of key starch-hydrolyzing enzymes such as α -amylase, alcohol dehydrogenase1 (ADH1) and pyruvate decarboxylase (PDC) followed by late rise in ethylene accumulation are together closely linked with improved AG (Ismail et al., 2009). Important aspects contributing to rice AG abilities

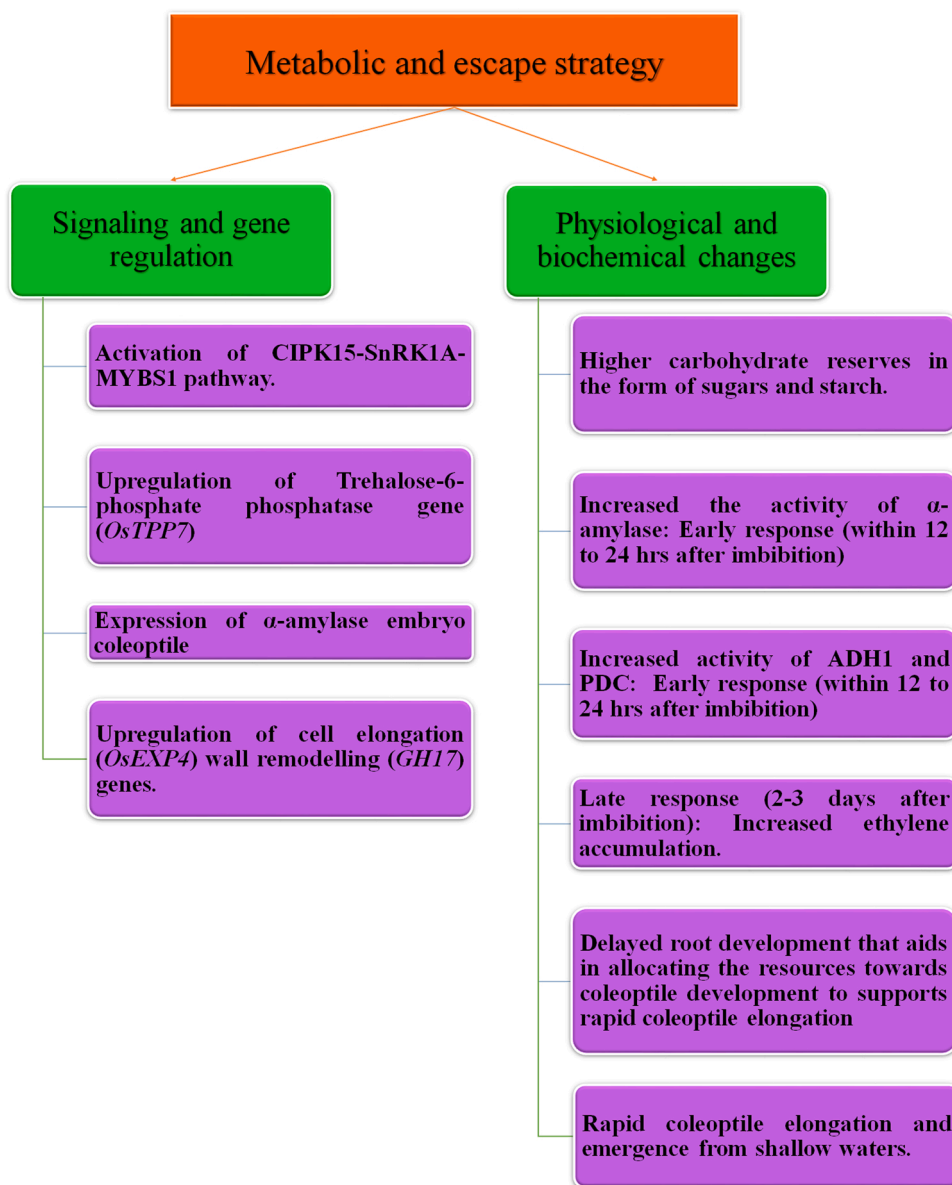


Fig. 1. Mechanisms regulating germination stage submergence tolerance in rice. CIPK15-SnRK1A-MYBS1 (CIPK15- Calcineurin B-Like (CBL) Protein-Interacting Ser/Thr PROTEIN KINASE; SnRK1A- Sucrose nonfermenting 1-Related protein Kinase 1A; MYBS1- Myeloblastosis (MYB) Sucrose 1) pathway induces or suppresses α -amylase expression.

when compared to other cereals are its soluble carbohydrate content, higher fermentation rates, and efficient energy use (Mustroph et al., 2006). Rice has ability to reprogramme its physiology and growth in response to O_2 deficiency, which has been confirmed through omic data linked with different metabolic and signaling routes. Transcript profiling of rice coleoptiles germinated under anaerobic conditions points towards a significant modulation of the transcripts responsible for carbohydrate assimilation and metabolism (Hsu and Tung, 2017). These modulations comprising of up-regulation of the enzymatic steps essential for pyruvate metabolism, up-regulation of genes encoding enzymes involved in cell expansion, and ethylene response factors, and a dramatic down regulation of gene encoding enzymes needing oxygen for their activity, suggests presence of a strategy that conserves energy required for upregulation of genes (Lasanthi-Kudahettige et al., 2007).

CIPK15 (Calcineurin B-like interacting protein kinase 15), is involved in sugar sensing during anaerobic germination besides promoting rice coleoptile elongation under low oxygen (Lee et al., 2009). Under complete submergence, lower ADH activity along with reduced

cell elongation and cell division during coleoptile growth was observed in ADH1-deficient rice mutants due to lower ATP levels (Takahashi et al., 2011). Under low O_2 conditions, sugar metabolism in both endosperm and embryo via glycolysis to ethanol fermentation needs higher ADH1 activity (Takahashi et al., 2014). Kretzschmar et al. (2015) identified OsTPP7, a trehalose-6-phosphate phosphatase gene, that modulates T6P/sucrose ratios which regulates the carbohydrates partitioning between the growing embryo and coleoptile tissues under anaerobic germination. Auxin regulated cell elongation is mainly credited for rapid coleoptile elongation under submergence (Kawai and Uchimiya, 2000). During germination under anoxic conditions, gene expression studies have revealed upregulation of expansin genes (Lasanthi-Kudahettige et al., 2007; Huang et al., 2000; Cho and Kende, 1997). In AG, high carbohydrate storage plays a key role i.e., varieties with AG potential have higher reserves of carbohydrates in the form of starch and sugars that supports germination under anoxic conditions (Raymond et al., 1985). To support rapid coleoptile elongation, root development is delayed thereby aiding in allocating the resources

towards coleoptile development. As coleoptiles approach the water surface, root growth is initiated due to higher O₂ levels (Ismail et al., 2009), indicating that root development is facilitated due to O₂ acquisition post coleoptile rapidly reaching the water surface. Different mechanisms regulating germination stage submergence tolerance in rice have been summarized in Fig. 1. Nevertheless, the thorough understanding on mechanism of tolerance to AG demands more scientific insights; hence, research efforts are in progress globally to reveal the underlying mechanism.

2.2. Vegetative stage submergence tolerance mechanisms (quiescence strategy)

In lowland flood prone areas, rice plants are more regularly submerged for approximately 1–2 weeks. Most rice cultivars, when submerged due to flash floods, elongate their leaves towards water surface for oxygen. However, due to large amount of energy requirement for shoot elongation, such cultivars cannot survive after water level recedes, leading to loss of yield. The underlying physiological mechanisms of rice plants tolerant to vegetative stage submergence due to flash floods are different from that adopted for anaerobic germination and deep-water flooding. Some varieties of Indica spp. survive submergence due to flash floods by adopting a unique “quiescent strategy” i.e., they suppress their growth to save valuable carbohydrate reserves until the water retreats, and later use this conserved energy for recovery and regeneration once floodwater recedes. In this adaptive strategy, the submerged stem undergoes minimal or no elongation (Sarkar, 1998; Almeida et al., 2003; Panda and Sarkar, 2014). A typical indigenous landrace, FR13A, possess the major QTL Submergence 1 (*SUB1*) that contributes for major phenotypic variation (about 70 %) of the flash flood submergence tolerance (Xu and Mackill, 1996; Toojinda et al., 2003) (Table 1). The relevant region responsible for this significant phenotypic variation was narrowed down by biparental linkage mapping which comprises a group of transcription factor genes of *AP2/ERF* (*APETALA2*/Ethylene Response Factor) super family, *SUB1A*, *SUB1B*, and *SUB1C* (Xu and Mackill, 1996). Out of these three genes, *SUB1A* is the gene that imparts tolerance to flash flood submergence (Xu et al., 2006). *SUB1A*, delays dark-induced senescence through the conservation of carbohydrate reserves and chlorophyll in the photosynthetic tissue (Fukao et al., 2012). The submergence tolerant allele *SUB1A-1*, at a site essential for its

protein function has a Single Nucleotide Polymorphism (SNP) responsible for an amino acid substitution (Singh and Sinha, 2016; Xu et al., 2006). Since introgression of the *SUB1A-1* allele does not have serious effect on grain yield and quality while providing flash flood tolerance, hence, it has been extensively used to develop varieties tolerant to flash floods in several countries of Asia (Bailey-Serres et al., 2010).

2.2.1. Quiescence Strategy of flash flood tolerance

Many researchers have investigated the molecular mechanism behind the *SUB1A* mediated quiescent strategy in rice (Voeselek and Bailey-Serres, 2015; Bailey-Serres and Voeselek, 2010) (Fig. 2). *SUB1A* belongs to group VII of the *AP2/ERF* (*APETALA2*/ethylene-responsive element binding factors) super family (*ERFVII*), whose members are highly conserved submergence-up-regulated genes in angiosperms (Reynoso et al., 2019). Introgression or over expression of *SUB1A-1* conferred significant submergence tolerance in the susceptible cultivars viz., Swarna and IR64 lines that lack *SUB1A-1* or have the *SUB1A-2* allele, but, due to a point mutation within the coding region *SUB1A-2* allele is non-functional (Xu et al., 2006; Fukao et al., 2006; Singh et al., 2009; Singh and Sinha, 2016). Transcriptomic approach was employed to elucidate the mechanism of *SUB1A-1*-mediated tolerance. This analysis revealed that the downstream genes related to hormone responses, anaerobic respiration and antioxidant systems were regulated by *SUB1A* (Jung et al., 2010; Locke et al., 2018). Under submergence, due to surrounding water, endogenous ethylene in rice is entrapped, which in turn leads to its accumulation in rice tissue (Sasidharan and Voeselek, 2015). Higher endogenous levels of ethylene results in reduction of ABA levels by inducing an abscisic acid (ABA) degradative enzyme (Saika et al., 2007), which results in enhanced responsiveness to GA and subsequent shoot elongation (Kende et al., 1998). Ethylene induces expression of *SUB1A-1* (Xu et al., 2006), however, *SUB1A-1* restricts both ethylene production and GA responsiveness, that suppresses elongation of shoot in flash flood-tolerant rice under submergence (Fukao and Bailey-Serres, 2008; Fukao et al., 2006). GA responsiveness is reduced due to *SUB1A-1* induced accumulation of GA repressor protein such as Slender Rice1 (*SLR1*) (Fukao and Bailey-Serres, 2008). *SUB1A* is also known to differentially regulate brassinosteroid (BR) pathway to mediate submergence tolerance response in rice. *SUB1A-1* induces transcriptional regulation of BR biosynthetic genes resulting in increased brassinosteroid levels after submergence, which in turn

Table 1
Identified traits, QTLs and genes that improve submergence tolerance in rice.

Trait	QTL	Gene and annotated protein	Chromosome	Tolerance mechanism	Reference
Flash flood tolerance	qSUB1 (Sub1)	<i>SUB1A</i> AP2/ERF family transcription factor	9	Reduced elongation growth and carbohydrate consumption during submergence	Xu and Mackill, 1996; Xu et al., 2006
	qTIL12	SNORKEL1 (SK1), SK2 AP2/ERF family transcription factor	12	Rapid elongation of internodes (20–25 cm/day) that can reach upto a length of several meters in deep water to escape submergence	Hattori et al., 2007; Hattori et al., 2009
Internode elongation	qTIL1	SD1 (OsGA20ox2) Gibberellin 20-oxidase	1	SD1 protein directs increased synthesis of gibberellins, largely GA4, which promotes internode elongation	Hattori et al., 2007; Kuroha et al., 2018; Pedersen et al., 2009; Winkel et al., 2013; Kurokawa et al., 2018
Underwater Photosynthesis	LGF1	OsHSD1 C30 primary alcohol synthesis	11	Leaf gas films facilitates gas exchange, supply of carbohydrates to roots for survival, regeneration and growth	Angaji et al., 2010; Kretzschmar et al., 2015; Panda and Sarkar 2012; Singh et al., 2014
Anaerobic germination	qAG-9-2	OsTPP7 Trehalose-6-phosphate phosphatase	9	OsTPP7 modulates T6P/sucrose ratios which regulate the partitioning of carbohydrate reserves to the actively growing embryo and coleoptile tissues under anaerobic germination	
Speedy recovery post submergence	Not mapped	AGPPase (ADP glucose pyrophosphorylase)	Not assigned	AGPPase facilitates greater accumulation of non-structural carbohydrates (NSC) which is available for speedy recovery post submergence	

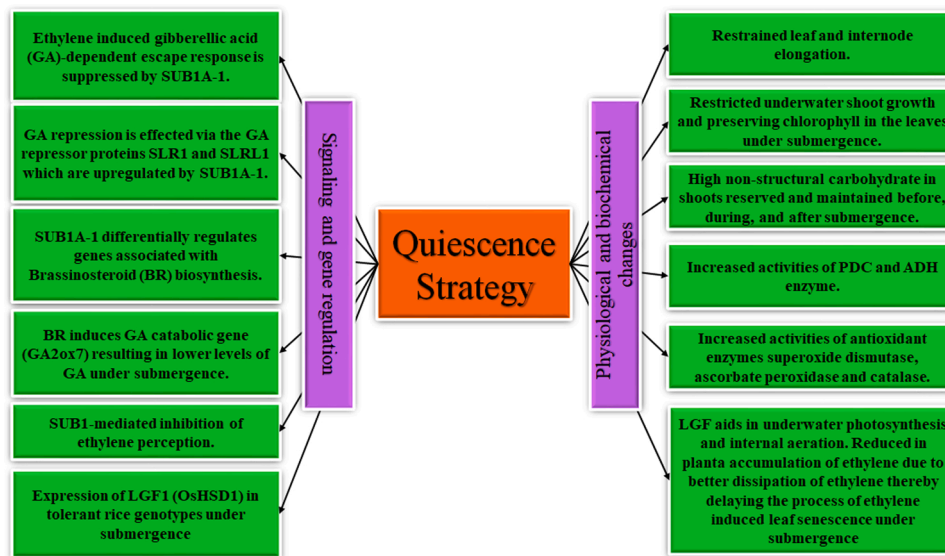


Fig. 2. Mechanisms regulating vegetative stage flash flood submergence tolerance in rice. SLR1 = SLENDER RICE1; SLRL1-SLR-LIKE1, both are negative regulators of GA signaling. LGF1= Leaf Gas Film 1.

induces GA catabolic enzyme OsGA2ox7 that suppresses GA levels (Schmitz et al., 2013). Recently, MAPK signal transduction network has been implicated in the functioning of *SUB1A-1* protein. It is involved in imparting submergence tolerance by facilitating the phosphorylation of the *SUB1A-1* during submergence, and directly regulating its expression through a *MPK3-SUB1A1* positive regulatory loop (Singh and Sinha, 2016). Das et al. (2005) reported that levels of non-structural carbohydrates (NSC) maintained during post submergence, was the pooled result of both the amount used during submergence and initial level before submergence. A high quantity of NSC pre and post submergence is very important for continuous supply of energy for active metabolism during and post-submergence recovery respectively (Das et al., 2005, 2009; Sarkar and Panda, 2009). Tissue specific expression studies using *SUB1A-1* promoter driven GUS reporter gene revealed the specific role of *SUB1A-1* in suppressing leaf elongation under submergence stress in the tolerant plants (Singh et al., 2010). To further understand the complex mechanisms of *SUB1A-1* mediated quiescent strategy of submergence tolerance, further study of ERFVII downstream genes is needed.

2.2.2. Role of leaf gas film (LGF)

Besides *SUB1A-1* mediated submergence tolerance through forcing quiescence on rice seedlings, leaf gas film on hydrophobic cuticles during submergence was known to be an adaptive mechanism to enhance plant gas exchange under water (Colmer and Pedersen, 2008; Pedersen et al., 2009). Due to hydrophobic surface, rice leaves can maintain a thin layer of gas on the surface, which allows maintaining respiration and photosynthesis under submergence. Leaf surface consists of different structures such as the papillae, and epicuticular waxes that are the major contributors to leaf hydrophobicity (Kotula et al., 2009; Ensikat et al., 2011). Leaf hydrophobicity in rice is mainly due to epicuticular wax platelets on the leaf surface (Koch and Barthlott, 2009; Herzog et al., 2018). Kurokawa et al. (2018) identified Leaf Gas Film 1 (LGF1) as the gene responsible for leaf gas films in rice. LGF1 regulates synthesis of C30 primary alcohol, which is essential for leaf hydrophobicity and gas films on submerged leaves (Fig. 2). Underwater photosynthesis increased by 8.2 fold due to leaf gas film, contributing to submergence tolerance (Kurokawa et al., 2018). A recent study reported that the presence of *SUB1* in the genetic background influenced LGF thickness and it was also shown that LGF resulted in reduced *in planta* accumulation of ethylene due to its better dissipation, thereby delaying

the process of ethylene induced leaf senescence under submergence (Chakraborty et al., 2020).

2.3. Vegetative stage submergence tolerance mechanisms (escape strategy)

During the rainy season, periodic flooding is a regular phenomenon in South and Southeast Asia resulting in stagnant water upto 2 m deep for several weeks. To adapt to this kind of periodic flooding, deep-water rice has developed an escape strategy (Catling, 1992). Mechanism of tolerance to deepwater stagnation in rice differs from flash floods induced submergence tolerance. Deepwater rice in shallow water grows normally but with rising water levels during heavy floods, it increases its height. To escape anoxic or hypoxic conditions, deepwater rice cultivars are capable of increasing their height by about 25 cm d⁻¹ so as to maintain contact with the air and light for photosynthesis (Bailey-Serres and Voesenek, 2008; Vergara et al., 1976). In contrast to the submergence tolerant rice varieties that enter into a quiescence mode by conserving storage carbohydrates, in deep water flooding, tolerant rice varieties use stored carbohydrates as the source of energy for the elongation of stem. Physiological and transcriptome analysis have revealed the role of plant hormones viz ethylene, abscisic acid (ABA), gibberellic acid (GA), and jasmonic acid (JA) in the deepwater response (Minami et al., 2018; Kende et al., 1998). Studies involving genetic manipulation and hormone application have assisted in unravelling the physiology of the deepwater flooding response in rice. Ethylene biosynthesis is activated in rice plant upon submergence, which in turn controls gibberellic acid and ABA synthesis. Internode elongation is positively regulated by Ethylene and GAs, while JA and ABA are believed to act antagonistically to GA-induced internode elongation. It is the ratio of gibberellic acid/ABA that determines whether a plant follows the strategy of quiescence or stem elongation (Das et al., 2005; Sauter, 2000; Kende et al., 1998). In deepwater rice, increased ethylene concentration in stems triggers synthesis of gibberellic acid and subsequent internode elongation (Hattori et al., 2009 and Métraux and Kende, 1983), but in non deepwater rice varieties, no such internode elongation is induced by ethylene. Under hypoxic conditions, 1-Aminoacyclopropane 1-carboxylate synthase (ACS) activity was induced, which is a key enzyme in ethylene biosynthesis pathway (Zarembinski and Theologis, 1997; Cohen and Kende, 1987). Role of ACC synthase (ACS) in the rapid stem elongation of deepwater rice have been confirmed by expression studies

on OsACS1 and OsACS5 genes (Van der Straeten, 2001; Zarembinsky and Theologis, 1997). Expansins, proteins known to mediate long-term extension of isolated cell walls, contribute to the growth of the major vegetative organs of rice and ultimately to survival of deepwater rice under submergence (Cho and Kende, 1997). Rapid internode elongation was also attributed to GA induced expression of α -expansin and β -expansin genes (Lee and Kende, 2001, 2002; Fig. 3).

Three major and two minor QTLs have been identified to be associated with the deepwater response through genetic linkage analysis studies (Nemoto et al., 2004; Tang et al., 2005; Hattori et al., 2008; Kawano et al., 2008; Nagai et al., 2012). Hattori et al. (2009) identified SNORKEL1/SNORKEL2 (SK1/2) genes that initiates deepwater response by encoding ERFs involved in ethylene signaling. SK1/2 are absent in other cultivated rice but, found only in deepwater rice varieties (Zhao et al., 2018; Hattori et al., 2009). The SK1/2 regulated downstream factors are yet to be known. *SUB1* locus, also consists of a cluster of three OsERFVIIIs that are related to SK1/2 but works differently (Xu et al., 2006).

ERFVIIIs SNORKEL1 and 2 transcriptionally regulates the escape strategy in certain deepwater cultivars while in other varieties, transcription factor OsEIL1 regulates gibberellin production (Hattori et al., 2009; Kuroha et al., 2018). In each of these above cases, the deepwater rice plant adapts to flooding by stimulating internode elongation to grow above the water level, thereby preventing the onset of hypoxia in cells due to gas exchange with the atmosphere. Recently, Kuroha et al. (2018) through a combination of genome-wide association (GWAS) and linkage mapping studies identified SEMIDWARF1 (SD1) (Table 1) as a gene that is responsible for promoting internode elongation in response to submergence. SD1 encodes OsGA20ox2 (O. sativa gibberellin 20 oxidase 2), that mainly catalyzes the biosynthesis of gibberellin, leading to the increased levels of bioactive GA₄, which is known to promote greater internode elongation than that of GA₁. In deep water rice-specific haplotypes, upon submergence higher levels of SD1 transcripts were accumulated which was independent of SK1/2 but found to work in synergy with SK1/2 in promoting internode elongation (Kuroha et al., 2018). Based on their study, Kuroha et al. (2018) proposed “ethylene-gibberellin relay” a model of signaling mechanism for internodal elongation under submergence in deepwater rice. Gomez-Ariza et al. (2019) recently reported the transcription factor Premature Internode Elongation 1 (PINE1) that increases GA responsiveness and subsequent internodal elongation. Further understanding of the GA-mediated deepwater response needs to be generated through discovery of QTLs

for GA responsiveness and their relationships with PINE1 in deepwater rice.

3. Management approaches for enhancing resilience towards submergence

Being a semi-aquatic plant, rice elongates its submerged shoot organs at faster rate and develops aerenchyma, which facilitates sufficient internal transport of oxygen to submerged parts (Magneschi and Perata, 2009), and consequently alleviates stress caused by anaerobic condition (Setter et al., 1997; Jackson and Ram, 2003). Submergence/ flooding conditions in rice field during seed germination can be a result of many factors like early, high and erratic rainfall, uneven field leveling, or deliberately flooding (after sowing) for weed suppression (Magneschi and Perata, 2009; Kumar et al., 2016a,b; Roy et al., 2011). Although rice shows tolerance to anaerobic environment during seed germination, however, this anoxic rice germination is only limited to its coleoptile emergence (rather root development) and partial growth, which is not enough to tolerate this stress (Magneschi and Perata, 2009). During submergence, rice seed germination undergoes alcoholic fermentation that supplies energy for normal respiration under limited oxygen. This energy facilitates rice seed germination that leads to rapid elongation of coleoptiles, and as a result the shoots comes out of the water surface and thus overcomes this anaerobic stress (Ismail et al., 2009). When coleoptile emerges above water surface, the scavenging of reactive oxygen species (ROS) begins (Ismail et al., 2009, 2012; Kirk et al., 2014; Colmer et al., 2014). These processes lead to survival under the hypoxic or anoxic conditions (Miro et al., 2017).

As puddle-transplanted rice is water, energy and labor intensive system, hence it is gradually being replaced by direct seeded rice (DSR) as the demand for water, energy and labour for DSR is comparatively less (Kumar et al., 2019, 2017). However, the success of DSR is challenging in rainfed areas, as flooding and/or water-logging in these areas is a common phenomenon which cause complete crop establishment failure (Ismail et al., 2009, 2012; Angaji et al., 2010). Although, under anaerobic condition rice seeds germinate by virtue of coleoptiles elongation, but is unable to develop roots and leaves (Ella and Setter, 1999). Varieties capable to germinate even in flooded soil condition could be beneficial for DSR system in rainfed and irrigated systems, where early flooding can check weed growth (Ismail et al., 2012, 2013). Anaerobic germination tolerant genotypes of rice could overcome the problem of crop establishment (under flooded/ submerged condition) associated in

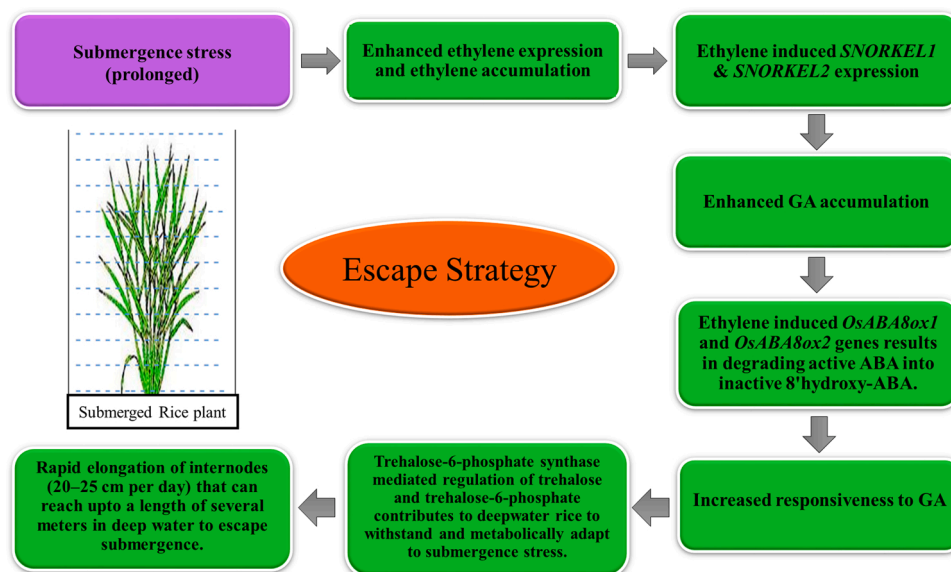


Fig. 3. Mechanisms regulating vegetative stage submergence tolerance (several weeks to months long) in rice.

DSR. These genotypes break starch into simple sugars at a faster rate and have faster germination and coleoptiles elongation (Miro et al., 2017).

3.1. Agronomic management for submergence tolerance

3.1.1. Selection of suitable variety

It was early 1940s and 1950s that the landraces with submergence tolerance were first reported (Fig. 4). The accessions FR43B and FR13A from Odisha, India and Goda Heenati, Thavalu, and Kurkaruppan from Sri Lanka were known for complete submergence tolerance (Mackill, 1996; Vergara and Mazaredo, 1975). In 1940s, FR13A was selected from the local Indica cultivar Dhallaputia from Odisha, India and its seeds were collected and preserved at IIRI seed bank during early 1960s and systematically screened for submergence tolerance in the 1970s. FR13A stood out as exceptionally tolerant to submergence stress with nearly 100 % of 10-day-old seedlings surviving 7 days of complete submergence (HilleRisLambers and Vergara, 1982; Vergara and Mazaredo, 1975). Breeding for submergence tolerance began in late 1970s and by early 1980s, high yielding varieties with submergence tolerance were developed, but their agronomic performance was poor. A complete timeline of research accomplishments in the last seven decades that led to understanding of submergence tolerance and release of mega-rice varieties with submergence tolerance in Asia is presented in Fig. 4.

Anaerobic germination tolerant rice genotypes can be a viable option, where early flooding or submergence prevails (Chamara et al., 2018), as these anaerobic condition not only suppresses weeds but also reduces rice seed germination. Under flooded conditions, AG tolerant genotypes need an optimum temperature (24–26 °C) for seed germination and seedling survival, as alpha-amylase activity decreases both in low and high water temperatures. These genotypes were found to be less affected by low O₂ and light transmission in water (Ella et al., 2010). Under submergence condition some of the AG-tolerant varieties like Ciherang AG1+Sub1 and IR 64 + AG1 were found to perform better in terms of seedlings/m² and stand establishment as compared to local check variety in Sri Lanka (Illangakoon et al., 2018). Researchers introgressed submergence tolerance *SUB1A* QTL in submergence intolerant rice cultivars to impart submergence tolerance in them (Fukao et al., 2006; Septiningsih et al., 2009). These rice cultivars showed better survival under submergence (Panda and Sarkar, 2012) as it maintained

higher activities of alcohol dehydrogenase and low rate of chlorophyll degradation in comparison with non *SUB1A* cultivar (Sarkar et al., 2014). To harness the benefits of *SUB1A* QTL, many submergence tolerant varieties like ‘Swarna *SUB1*’ were bred through marker-assisted back crossing (Neeraja et al., 2007). Later, many mega varieties tolerant to submergence, viz. Samba Mahsuri *SUB1*, IR64 *SUB1*, CR1009 *SUB1*, BR11 *SUB1* and Thadokkam1 *SUB1* were developed (Singh et al., 2009). Swarna *SUB1* was then released in Bangladesh, India and Indonesia; in Bangladesh, BR11 *SUB1* was released; and in Philippines and Indonesia, IR64 *SUB1* was released (Sarkar, 2012). Despite having this tolerance, these varieties cannot be used in direct seeding of rice because of their sensitivity towards limited oxygen during germination. Imparting AG tolerance to these high-yielding varieties will enhance yield under submerged condition and ultimately will lead to increased profitability of rice farmers (Lal et al., 2018). DSR encounter yield loss due to severe weed competition, where it can reach up to 100 % yield loss in absence of control measures (Rao et al., 2007; Mahajan and Chauhan, 2013). It was found that the AG lines showed higher germination percentage and gave better performance under varying flooding stress. Varieties like IR64-AG NILs (IR64-AG131 and IR64-AG132 AG tolerant but submergence intolerant) were observed to be have 121 % and 98 % higher germination compared to IR64-Sub1 (submergence tolerant; AG intolerant), and IR64 (submergence & AG intolerant) respectively (Lal et al., 2018). Besides anaerobic germination, plant types with moderate stem elongation, owing to their slower rates of metabolism are considered suitable for flood-prone lowland and submerged conditions (Setter and Laureles, 1996; Sharma, 1999).

With the help of modern molecular marker technologies, it is now possible to map and clone the genes for submergence tolerance. Several traits linked with flood tolerance in rice have been well studied and QTLs have also been identified for these traits (Fig. 5). Among various types of flooding stress, due to its unique stem elongation ability, deepwater rice captured the attentions of rice geneticists first. For the evaluation of deepwater traits, total internode length (Vergara and Mazaredo (1978) and position of the lowest elongated internode (Inouye, 1983) were proposed. Xu and Mackill (1996) mapped a major QTL *SUB1* on rice chromosome 9 for vegetative stage submergence tolerance in FR13A, which was responsible for nearly 70 % of the phenotypic variation (Table 1). Different QTL mapping studies for

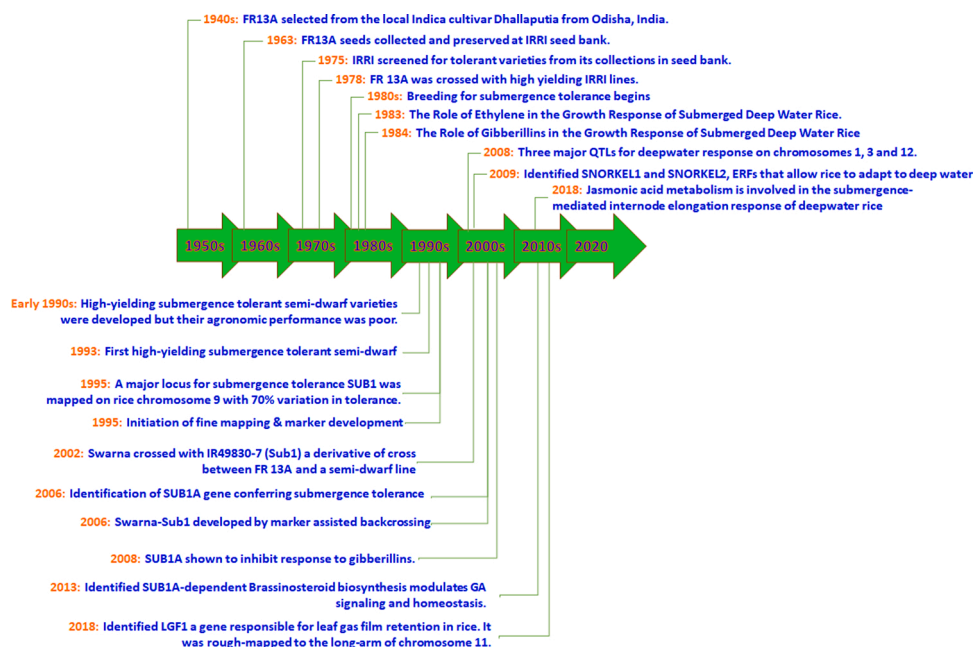


Fig. 4. Timeline of research accomplishments in the last Seven decades that led to understanding of submergence tolerance and release of mega-rice varieties with submergence tolerance in Asia.



Fig. 5. A summary tree showing works of QTL mapping studies for submergence tolerance traits in rice. VSST = vegetative stage submergence tolerance; LGF = Leaf Gas Film; CE = coleoptile elongation; TIL = total internode length; AG = Anaerobic germination; LEI = Lowest elongated internode; RIE = Rate of internode elongation; IE = Internode elongation; NEI = Number of elongated internodes.

submergence tolerance traits are summarized in Fig. 5.

3.1.2. Seed rate

Direct seeded crop before the onset of monsoon has better submergence tolerance as compared to recently transplanted crop (Sharma, 1995a). Submergence generally leads to poor rice seedling establishment, which can be compensated with use of optimum or higher seed rate in DSR (Sharma and Ghosh, 1998; Lal et al., 2018) and seedlings area⁻¹ in transplanted rice (Reddy et al., 1990) as depicted in Table 2, Fig. 6. Illangakoon (2018) emphasized that high seeding rate (100 kg ha⁻¹ as compared to 60 kg ha⁻¹ under DSR) and introducing better AG-tolerant varieties can attribute to better crop establishments (13–15 % increment) as well as panicle densities (15 %) and consequently give higher grain yield under submerged condition. These findings support the findings of Lal et al. (2018), where increasing seed rate significantly increased emergence and seedling establishment under DSR, and highest increment was with use of AG tolerant genotypes. Higher seed rates, improved seeding methods and nutrient application enhance tolerant genotype production efficiency by boosting germination, early growth and partitioning of photosynthates to different plant parts (Ashraf and

Foolad, 2005). The practice of high density seeding (under DSR), vigorous seedling (under TPR) and basal N fertilization (Sharma and Ghosh, 1999) has the potential to enhance yield of lowland rice prone to submergence. However, higher seed rate may lead to intense interplant competition, and under excessive flooding the situation becomes worst due to loss of plant dry matter. This loss can be compensated with higher rate of N fertilization (Reddy et al., 1986), as increase in N-fertilizer dose along with higher seed rate suppress tiller mortality and increase panicle weight (Sharma and Ghosh, 1998). During nursery raising, lower seeding density resulted into better root length and dry matter accumulation in seedlings that consequently gave higher yield (Bhowmik et al., 2014). This may be due to better seedling vigour (Kumar et al., 2012) as it is directly linked to tillering ability and grain yield of rice (Tekrony and Egli, 1991). Plant geometry and density also affects yield of hybrid rice exposed to submergence condition. Islam et al. (2013) reported higher yield under plant geometry of 20 × 10 cm and one seedling hill⁻¹ (Table 3), whereas, more seedlings and less spacing create competition among plants.

Table 2
Role of seed rate in enhancing grain yield under submergence stress.

Submergence depth and duration	Varieties	Seed rate (kg ha ⁻¹)	Yield (t ha ⁻¹)	Location	Reference
5 cm (5–21 days)	IR64	40 vs 60	1.84 vs 2.09 (14 %↑)	NRRI, Cuttack, Odisha, India	Lal et al., 2018
	IR64-Sub1		2.29 vs 2.49 (9%↑)		
	IR64-AG131		3.59 vs 3.71 (3%↑)		
	IR64-AG132		3.64 vs 3.80 (4%↑)		
	IR64 vs IR64 SUB1	40	1.84 vs 2.29 (24 %↑)		
	IR64 vs IR64-AG132	40	1.84 vs 3.64(98 %↑)		
	IR64 vs IR64-SUB1	60	2.09 vs 3.80(82 %↑)		
5 cm upto 21 days	Bg 366	60 vs 100	2.3 vs 4.5 (95 %↑)	RRDI, Ibbagamuwa, Sri Lanka	Illangakoon et al., 2018
	CiherangAG1+SUB1		2.0 vs 4.0 (100 %↑)		
	IR 64 + AG1		2.1 vs 2.8(33 %↑)		
			1.92 vs 2.28 (19 %↑)		
Fluctuating depth (between 5–99 cm)	Nalini	22 vs 44*	2.28 vs 2.40 (5 %↑)	NRRI, Cuttack, India	Sharma and Ghosh, 1998
		44 vs 88	2.40 vs 2.71 (13 %↑)		
		88 vs 132	2.71 vs 2.68 (1%↓)		
		132 vs 176	2.93 vs 3.02 (3%↑)		
Natural submergence throughout the season	Gayatri	88 vs 132	2.93 vs 3.02 (3%↑)	NRRI, Cuttack, India	Sharma and Ghosh, 1999
	Swarna Sub-1	25 vs 40 g/m ² (Nursery)	5.29 vs 4.86 (8%↓)		
Natural submergence (twice- 40–50 cm depth for 6 days & 30–40 cm depth for 4 days)	S-201	120 vs 240	8.68 vs 9.5 (9 %↑)	Colusa, California, US	Miller et al., 1991
		240 vs 480	9.5 vs 9.98 (5 %↑)		
		480 vs 840 (seeds/m ²)	9.98 vs 10.58 (6%↑)		

* (1000 grain weight of variety Nalini =22 g; seeds m⁻² converted to kg ha⁻¹-seed rate). ↑ = increase, ↓ = decrease.

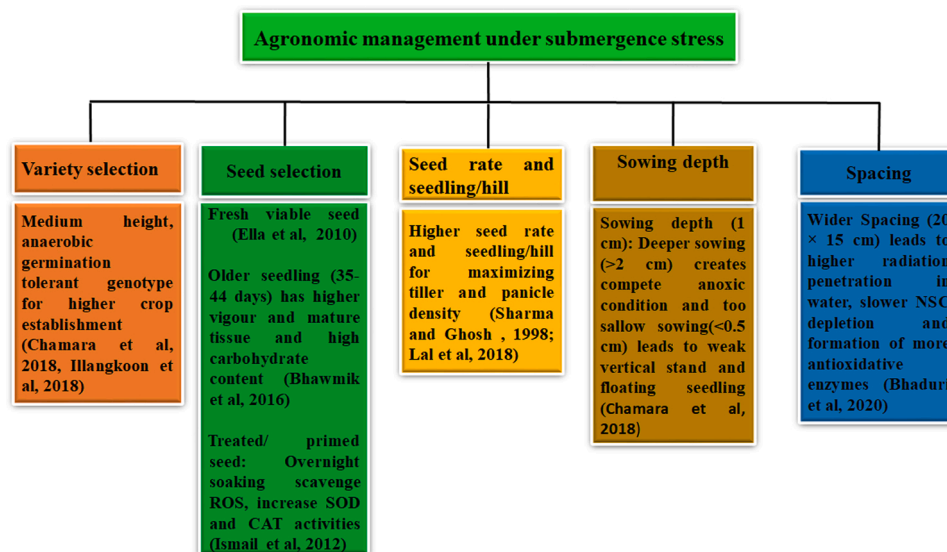


Fig. 6. Agronomic management strategies for maximizing yield under submergence stress.

3.1.3. Seed priming

Seed priming is a regulated hydration process, wherein the seeds are soaked in water or any suitable solution and re-dried to its original state in such a way so that the germination related metabolic activities starts, but radical emergence does not initiate. It helps the seedling to perform

better under adverse condition such as extreme temperature and excess moisture by triggering germination at rapid and uniform rate (Bradford, 1986; Farooq et al., 2006a, 2019; Ella et al., 2010; Ismail et al., 2012; Javed et al., 2021; Mei et al., 2017). Hussain et al. (2016) reported a significant increase in seed developmental process, when rice seeds were

Table 3
Role of crop geometry in enhancing grain yield under submergence stress.

Submergence duration and depth	variety	Crop Geometry	Grain yield (t ha ⁻¹)	Location	References
Natural submergence (twice- 40–50 cm depth for 6 days & 30–40 cm depth for 4 days)	Swarna Sub-1	Seedling age (days) 30 vs 44	4.92 vs 5.23 (6%↑)	Rice Research Station, Chinsurah, WB	Bhawmick et al., 2014
5–7 cm continuous flooding	Koshihikari	Seedling age (days) 14 vs 21	7.93 vs 7.66 (3 %↑)	Chiba, Japan	Chapagain and Yamaji, 2010
5–7 cm continuous flooding	Koshihikari	Spacing (cm) 30 × 30 cm vs 30 × 18 cm	8.01 vs 7.58 (5 %↓)	Chiba, Japan	Chapagain and Yamaji, 2010
10–12 cm continuous standing water	Aloran (hybrid variety)	Spacing (cm) 25 × 20 cm vs 20 × 10 cm	4.3 vs 7.5 (74 %↑)	BRAC, Bangladesh	Islam et al., 2013
10–12 cm continuous standing water	Aloran (hybrid variety)	Seedling/hill 1 vs 2 seedling 1 vs 3 seedlings (Spacing-20 cm × 15 cm)	5.5 vs 6.4 (16 %↑) 5.5 vs 5.9 (7 %↑)	BRAC, Bangladesh	Islam et al., 2013
Natural submergence	Gayatri	Seedling/m ² 115 vs 155	2.93 vs 3.02 (3 %↑)	NRRI, Cuttack, India	Sharma and Ghosh, 1999

exposed to with 60 μM selenium (chemical priming) and 100 mg L⁻¹ salicylic acid (hormonal priming) for enhancing submergence tolerance in rice. Hydro-priming as a seed treatment was found to improve the survival of rice seeds by about 40 % as compared to non-primed seed by increasing the activity of α-amylase, soluble sugars synthesis and starch degradation (Illangakoon et al., 2016; Mulbah and Adjetey, 2017). Iron-coated primed rice seeds exhibit better seed germination qualities as compared to unprimed and non-iron coated rice seeds (Mori et al., 2012). Hormone priming (salicylic acid at 150 ppm), significantly increased the tiller by 53 % over control (Kareem et al., 2013), whereas Osmotic priming (PEG at 40 %) significantly increased the number of productive tillers per hill by 82 % above control (Kareem et al., 2013). Use of 2% of Jamun (*Syzygium cumini*) leaf extract improved establishment of seedling under flooded condition (Sarkar, 2012). Seed priming affects the concentration of soluble sugars and starch in germinating rice seeds (Ella et al., 2010) as well as activities of many enzymes involved in germination process like total amylase and alcohol dehydrogenase (Farooq et al., 2006b; Sarkar, 2012). Appropriate seed coating agents is also helpful in thickening the pericarp, as pericarp cells have many protective phenolic compounds (Serna-Saldivar, 2010; Mora et al., 2013; Chamara et al., 2018; Afzal et al., 2020).

3.1.4. Seed/seedling age

When flooding or submergence is anticipated, then fresh and viable seeds should be used because flooding decreases survival percentage of old seeds due to decline in the concentration of antioxidant metabolites like superoxide dismutase (SOD) and catalase and increase in oxidative degradation of lipids (Ella et al., 2010). Aged seedlings has significant effect on crop in main field. After submergence, it affects crop survival, growth of crop stand, days to 50 % flowering and maturity, yield attributes and consequently grain and straw yields (Mishra and Salokhe, 2008; Himeda, 1994). Older seedlings (35–45 days) gave better performance (Table 3) in submerged situations as compared to younger ones (Gautam et al., 2017; Bhowmick et al., 2014). Younger seedlings when exposed to submergence exhibited less survival rate, growth after recovery, allometric parameters, carbohydrate content, and photosynthetic rate. Whereas, older seedlings were taller, sturdier, and healthier, had more mature tissues, greater dry biomass and carbohydrate storage at the time of transplanting, consequently, their tolerance level was improved (Singh et al., 2005; Ram et al., 2009; Bhowmick et al., 2014; Gautam et al., 2017).

3.1.5. Method and depth of sowing

Drum seeding of AG tolerant varieties as compared to broadcasting in DSR system has been reported to give higher yield (Lal et al., 2018). Santhi et al. (1999) and Narasimman et al. (2000) also reported

significantly higher number of panicles m⁻² and higher grain yield under drum seeding.

Sowing depth exhibits significant effect on the rice seedling emergence under flooding. Seed sowing at 2 cm depth was found to be more adversely affected in terms of crop establishment as compared to 1 cm or less (Chamara et al., 2018). In a flooded soil the redox potential near the soil surface is around +400 mv which decreases upto -300 mv at around 1 cm soil depth, however, beyond this depth, a sharp decline of oxygen is observed, which creates highly anaerobic or anoxic condition. The decrease in redox potential beyond 1 cm depth affect nutrient dynamics as well as accumulation of some phytotoxic compounds (Ponnamperuma, 1975; Armstrong and Drew, 2002; Pezeshki and De Laune, 2012) which consequently cause poor crop establishment.

Furthermore, a shallow sowing depth of 0.5 cm under flooded conditions, resulted into weak vertical stand of plants, possibly because of exposure of the upper portion of developing seedlings, above the soil surface. Hence, the rice plant stand becomes vulnerable to lodging even with slower external wind forces (Chamara et al., 2018). Additionally, too much shallow sowing (0.5 cm) leads to development of floating young seedlings above the water surface, because the elongation of coleoptiles develops more porous aerenchyma, which gives buoyancy to the seedlings (Vartapetian and Jackson, 1997; Magneschi and Perata, 2009; Miro and Ismail, 2013,) and this high buoyant force and lack of anchoring roots of seedlings leads to low crop establishment (Chamara et al., 2018).

3.1.6. Spacing

Wider spaced plants (row to row: 20 cm and plant to plant: 15 cm and more) showed more tolerance to submergence even under the 12 days of complete submergence. Compared to closer spacing, wider spacing led to higher underwater radiation penetration (thus higher photosynthesis and less senescence compared to closer spacing), higher initial non-structural carbohydrate (NSC) content, slower NSC depletion rate, and higher antioxidant enzyme for stress recovery (Bhaduri et al., 2020). The plant spacing and density for hybrid rice was optimized by Islam et al., 2013, who reported the optimum geometry as 20 × 10 cm and density as one seedling hill⁻¹ for getting highest yield under submergence condition.

3.2. Nutrient management for mitigating submergence stress

The influx of water during submergence causes loss of significant amount of nutrients due to several losses like runoff, volatilization, and deep percolation which not only causes nutrient deficiency in soil but also adversely affects the crop growth. Generally, rice farmers are of the opinion that rice crops exposed to submergence may not give response to

post flood applied fertilizers and hence, most of the farmers are reluctant to go for fertilizer application in the post flood scenario. Floodwater sometimes deposits, nutrient rich sediments and benefits the crops; however, the high fertility mainly benefits the succeeding post-flood crops. The submerged crops are significantly damaged by the floodwater which results in poor crop establishment (Sarangi et al., 2015). The mineral nutrient content of rice seedlings in adequate amount at both pre and post-submergence is necessary for coping the flooding stress, and quick post flood recovery (Singh et al., 2016). Under flash floods, rice plants are subjected to two drastic environmental changes: (i) During complete submergence, plants faces transition from aerobic to hypoxic condition and (ii) when the floodwater recedes they face transition from hypoxic to aerobic condition. For adaptation to these changing environments, the plant must have physiological mechanism to cope up the changes. Therefore, proper nutrient management for flood-prone areas may help the plant in production of metabolites, which may lead to better crop establishment. Application of nutrients particularly N, P and K under submergence/post submergence condition helps the rice crop in tiller regeneration, maintaining high chlorophyll and NSC, regulating enzyme activity and cation-anion balance (Table 4, Fig. 7). These morphological and physiological changes are instrumental in imparting greater stress resistance to plants (Gautam et al., 2014; Jackson and Ram, 2003; Marschner, 2012; Singh et al., 2018). This

Table 4
Effect of different nutrient application strategy on physiological and agronomical responses of rice subjected to submergence stress.

Nutrient application	Physiological and agronomical response	Reference
Post flood nitrogen application as foliar spray	<ul style="list-style-type: none"> • Spraying removes adhered silt particles from leaf surface • Maintains chlorophyll stability and assimilate partitioning • Increases antioxidant metabolite activity 	Gautam et al., 2014a, 2015; Panda et al., 1979; Ella and Ismail, 2006; Crafts-Brandner, 1992; Rios-Gonzalez et al., 2002; Shin et al., 2005; Kovacic and Backor, 2007; Slit, 1999; Jackson and Ram, 2003.
Basal phosphorus application	<ul style="list-style-type: none"> • Promotes better survival during submergence and recovery during post-submergence • Maintains initial seedling vigour and shoot carbohydrate concentration • Lowers ethylene accumulation during submergence 	Gautam et al., 2014b; Ramakrishnayya et al., 1999; Fukao and Bailley – Serres, 2008; Jackson and Ram, 2003.
Basal potassium application	<ul style="list-style-type: none"> • Maintains good growth and metabolism • Helps in activation of several enzymes • Enhances photosynthetic pigments and photosynthetic capacity • Helps in stomatal movement and turgor regulation • Increases plant nutrient uptake 	Demidchik, 2014; Shabala and Pottosin, 2014; Ashraf et al., 2011; Marschner, 2012; Singh et al., 2014; Cakmak, 2005; Gautam et al., 2014a, 2014b, 2016.
Basal silica application	<ul style="list-style-type: none"> • Prevents crop lodging and imparts erectness to leaves • Enhances N responsiveness of rice • Reduces stem elongation, leaf senescence, lodging, chlorosis and depletion of NSC • Alleviates many abiotic stresses like flooding, lodging, freezing etc. • Enhance antioxidant defence abilities 	Tamai and Ma, 2008; Ma et al., 1989; Munir et al., 2003; Ho et al., 1980; Lal et al 2015; Epstein, 1994; Marschner et al., 1990; Okamoto, 1969; Sadanandan and Vergese, 1969; Gautam et al., 2016.

clearly signifies the importance of proper nutrient management strategy for enhancing rice production and productivity in submergence-affected areas.

3.2.1. Nitrogen management

Adequate and timely nitrogen (N) fertilization promotes tillering and photosynthetic efficiency and decreases gaseous loss of N (Chatterjee et al., 2018). The improved photosynthesis enhances biomass production and ensures optimum grain yield even under complete submergence (Fig. 7). As a precautionary measure, to avoid damage to crop due to submergence, generally farmers apply N in nursery, which results in N enrichment of seedlings. During submergence, the higher N content in these seedlings results in more aboveground growth over belowground growth, which results in depletion of soluble carbohydrate stored in upper plant parts (Ella and Ismail, 2006). Besides, the high N content also increases the succulence/softness of shoots, which promotes shoot elongation. The higher shoot elongation confuses the plant with sense of ageing, which results in increased accumulation of ethylene in plant parts (Gautam et al., 2015). Thus, due to pre-submergence N application, the carbohydrate partitioning and shoot-root ratio is influenced adversely, which results in lower number of phyllochron and poor survival (Ella and Ismail, 2006; Gautam et al., 2014). For fast recovery under post submergence condition, plants need energy for maintenance and metabolism and this is primarily supported by stable chlorophyll system and higher levels of NSC (Das et al., 2005; Panda et al., 2008). Due to presence of turbidity in floodwater, there is deposition of silt particles on leaf surface. The silt particle blocks the stomata and hampers the stomatal conductance, which results in lower concentration of starch and sugar in leaves (Palada and Vergara, 1972). Post submergence foliar spray of urea removes the adhered silt particle from the leaf surface due to the force applied by the water-urea solution. The desilting of leaf surface enables the plants to regain optimum photosynthesis and better survival. Gautam et al., 2014; 2015 reported higher level of chl a and b, NSC, Pn rate which lead to higher plant survival when N was applied as foliar spray under post-submergence condition. They also reported a positive correlation between NSC and plant survival and negative correlation between shoot elongation and plant survival. These correlations established the importance of chlorophyll stability and higher NSC levels in plants for rapid recovery from submergence stress.

3.2.2. Phosphorus management

Mineral nutrition of phosphorus (P) is essential for optimum growth and development of rice. Generally, rice farmers avoid application of P, however, in submergence prone areas it is well proved that P application has the potential to mitigate the adverse effects of submergence (Table 4; Fig. 7). Right method of P application for better efficacy against submergence is application in the nursery and as basal dose in the main field before submergence rather in the floodwater. Addition of P in floodwater accelerates algal growth, and hence the submerged plant faces stress for CO₂ and light (Ramakrishnayya et al., 1999). Complete submergence increases ethylene synthesis and its accumulation in different plant parts, which is a major reason for chlorophyll degradation, leaf senescence, lowering of stomatal conductance and intercellular CO₂ concentration as well as denaturing of the photosynthetic machineries leading to lower photosynthetic rate of the submerged plants (Mackill et al., 2012; Ismail et al., 2012; Fukao and Bailey-Serres, 2008). Pre submergence application of P along with N, significantly increased initial seedling vigor and shoot carbohydrate concentration. It facilitated better survival and regeneration during post submergence recovery phase in several lowland rice varieties. Basal P application lowered ethylene accumulation in shoots during submergence and hence the photosynthetic rate was enhanced during post submergence recovery phase (Gautam et al., 2015; Ramakrishnayya et al., 1999).

3.2.3. Potassium management

Submergence induces significant reduction in stomatal conductivity

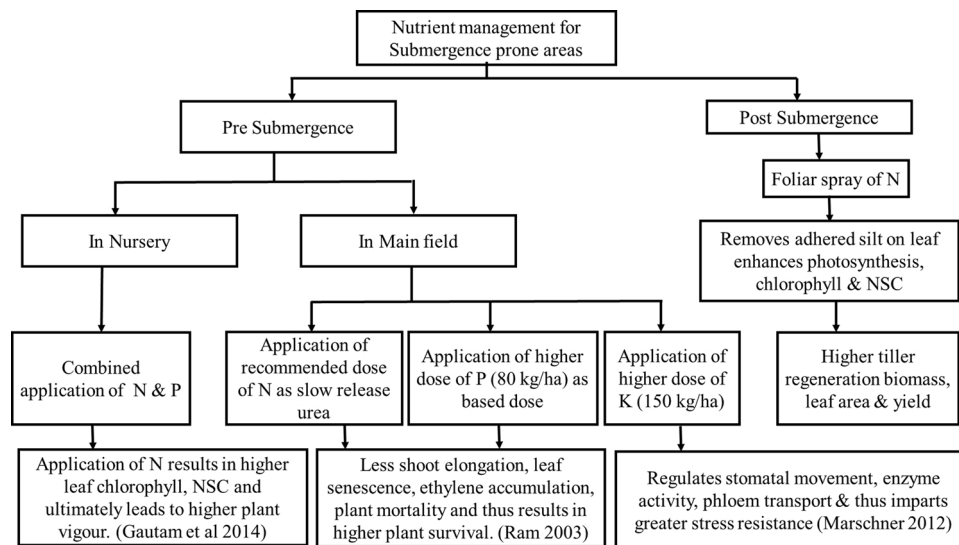


Fig. 7. Nutrient management strategies for maximizing yield under submergence.

(Pang et al., 2004; Polacik and Maricle, 2013) which affects the nutrient uptake to the aboveground plant parts (Table 4; Fig. 7). Under submergence, hypoxic/anoxic condition prevails, which immediately arrests the root functioning and leads to severe potassium (K) deficiency in the root (Marschner, 1995; Malik et al., 2002). Application of K imparts waterlogging/submergence resistance in plants by activating plant growth, metabolism and activity of several enzymes (Pang et al., 2006; Mugnai et al., 2011; Dwivedi et al., 2017). Exogenous application of K facilitates higher K^+ , Ca^{2+} , Mn^{2+} and Fe^{2+} accumulation and enhances plant growth, photosynthetic pigments and photosynthetic capacity that ultimately helps in mitigating the adverse effects of submergence (Ashraf et al., 2011). Application of K fertilizers increased antioxidant metabolite activity, and improved post submergence survival and recovery (Gautam et al., 2016; Cakmak, 2005). Thus, application of nutrients like K along with N and P has been proved beneficial for post submergence recovery and ensuring optimum grain yield.

3.2.4. Silicon management

Silicon (Si) plays a prominent role in enhancing lodging resistance and maintaining the erectness of leaves (Table 4). The erect posture of leaves permit higher light transmittance and thus enhances photosynthesis (Tamai and Ma, 2008). Application of higher dose of N fertilizer promotes lodging and thus limits the grain yield production. Use of Si along with N prevents the lodging of rice crop as it increases culm strength and leaf erectness (Ma et al., 1989; Munir et al., 2003). Silicon enjoys a synergistic relationship with N, and hence combined application of N and Si is known to augment productivity of lowland rice fields (Lal et al., 2015b; Mohanty et al., 2020, 2021). Researchers have proved that Si nutrition mitigate many abiotic stresses like flood, drought and freezing (Epstein, 1994; Kumar et al., 2019) by strengthening the cell walls of culms, hulls, leaves and roots. Moreover, Si helps in increasing the photosynthesis by maintaining erectness of rice leaves and clumps, which helps in greater light interception. Application of basal Si combined with post-flood N increased post flood recovery by increasing emergence of green leaf and leaf area index, ultimately leading to optimum grain yield. Silicon application helped in recovery of the partially damaged tillers, reduced elongation, lodging, leaf senescence, and chlorosis which led to higher survival percentage, enhanced photosynthetic rate, antioxidant metabolite activity and ultimately optimum grain yield (Sharma, 1995b; Lal et al., 2015a; Gautam et al., 2016).

4. Conclusions and future research needs

Major rice growing belts of the world suffer from the menace of submergence, which is likely to be aggravated under the anticipated climate change scenarios. Submergence tolerance being a complex trait, is influenced by several physiological or morphological characteristics. Early flood affects rice germination in the areas with wet and dry direct seeding, by creating hypoxic conditions, whereas flash flood affects rice crop severely by affecting its growth and development. Therefore, understanding the mechanisms of submergence tolerance in rice due to these different types of flooding at different growth stages is important to come up with innovative management practices for mitigating the adverse effects. At vegetative stage, when tolerant rice genotypes are subjected to flash flood induced submergence, they enter into a quiescence mode and utilize the non-structural carbohydrates once water level recedes after 10–14 days. Tolerance mechanism to flooding during germination stage comprises rapid elongation of the coleoptile to emerge from shallow waters to escape from submergence. Similar escape strategy is being identified as a mechanism in periodic flooding that causes several weeks to months long deep submergence.

Besides identification of landmark QTL for submergence tolerance *SUB1A*, and other QTLs like *LGF1*, *OsTTP7*, *SK1/2*, that led to development of submergence tolerant rice varieties, specific management practices have also been designed and developed for resilience to unfavorable conditions. To enhance the grain yield of flood-prone lowland rice various management practices like high-density seeding for DSR, vigorous seedling for TPR and basal N fertilization have been developed. Various seed priming practices have been very effective for ensuring higher seedling survival rate, emergence, shoot and root growth under flooded conditions. Nutrient management practices like application of N, P, and K under and/ post submergence aids in the recovery of rice crop by regenerating tillers, maintaining higher NSC content and regulating enzymatic activity. Productivity of lowland rice fields is very well augmented by combined application of N and Si due to their synergistic interactions.

With contemporary climate change predicted to trigger the incidence of flooding, cryptic genetic variation available in wild rice gene pools may help breeders to develop modern rice varieties having greater resilience towards submergence. Identification and introgression of landmark *SUB1A* gene led to development of submergence tolerant rice varieties that can withstand flash floods lasting upto two weeks. In addition, a recent study on deepwater rice-specific *SD1* haplotype, proposed ethylene-gibberellin relay model, which establishes direct

molecular link between ethylene signaling and gibberellin biosynthesis. This was confirmed by transcriptional gain-of-function allele of the Green Revolution semi dwarf (*SD1*) gene that triggered elongation of stem, enabling it to survive under flooding conditions (Kuroha et al., 2018). Utilisation of genetic factors like *OsTPP7* for anaerobic germination and periodic flooding will further aid in developing breakthrough rice varieties tolerant to flash flood induced submergence stress. Wild rice gene pools should be explored for identifying superior alleles of the *SUB1A* gene that can impart greater tolerance to submergence. With the advent of CRISPR/Cas system, genome-editing technologies have been drastically advanced (Doudna and Charpentier, 2014). These advanced technologies can be employed in crop improvement to facilitate functional modification of genes regulating useful traits. Efficient utilization of both conventional and new technologies like CRISPR/Cas can greatly help in developing climate resilient rice varieties. In summary, continuing the studies on understanding of unknown factors governing tolerance to various types of submergence stress and developing effective management practices and balanced use of both conventional and modern technologies will help in imparting submergence tolerance in modern rice varieties. Besides *SUB1A-1* mediated submergence tolerance, leaf gas film on hydrophobic cuticles during submergence is also known to impart tolerance against submergence stress. Rice genotypes should be evaluated for longer leaf gas film retention during submergence, to significantly increase underwater photosynthesis during prolonged submergence.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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