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Physiological, biochemical and molecular mechanism of submergence tolerance in rice (*Oryza sativa* L.)

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Abstract

Abiotic stresses adversely affect plant growth and productivity leading to a series of morphological, physiological, biochemical and molecular changes in plants. Submergence stress is one the major abiotic stresses that affects crop growth and yield. Above 16 million ha of rice lands of the world is affected due to submergence. Both partial and complete submergence confers some serious consequences in plants grown in flood prone areas. Some plants can tolerate these conditions by adopting various survival strategies. Among the cultivated plants, rice is the most efficient crop, which has the ability to survive under submergence for prolonged time. This review focuses on understanding the mechanism of submergence tolerance in rice on physiological, biochemical and molecular basis.

Keywords: Abiotic stress, submergence tolerance, rice

Introduction

Rice (*Oryza sativa* L.) is the most important food crop in the world, feeding more than 3 billion global populations. Rice as a staple food is increasingly becoming important in Africa and Latin America in recent years (IRRI Rice Knowledge Bank, 2013) [23]. Among all the cereals, rice is unique due to its ability to grow in wet environments with lots of climatic adversities where other crops cannot survive. Rice is mostly grown under five different ecologies viz. irrigated, rain-fed lowland, rain-fed upland, flood-prone deep water and coastal saline ecologies. Due to its distribution in diverse geographical locations rice faces many abiotic and biotic stresses throughout its life cycle. Abiotic stress is defined as the environmental condition in which the non-living factors or external factors have a negative impact on the living organisms. Among the 42 abiotic and biotic stresses affecting rice production, submergence is considered as the third most important constraint affecting production and productivity of rice, particularly in eastern India predominated by lowland and flood-prone deep-water ecologies (Setter *et al.*, 1998) [49]. Submergence is a type of flooding stress that affects functioning of plants at several levels which can lead to severe tissue damage and eventually mortality. Submergence has been divided into two types: complete submergence (the entire plant is fully immersed in water) and partial submergence (at least part of the terminal shoot remains above the water surface). Submergence results in slow gas diffusion, oxygen deprivation (Bailey-Serres *et al.*, 2014) [6]. Light availability is reduced due to turbid floodwaters which leads to a further decrease in underwater photosynthesis. Due to lack of efficient gas exchange, the rate of transpiration is restricted severely (Pedersen *et al.*, 1993) [40]. Under prolonged submergence there is faster rate of carbohydrate consumption and this creates an energy crisis that can be lethal. In addition, reactive oxygen species and toxic compounds such as organic acids, pyruvate accumulate and conversion of ethanol to acetaldehyde takes place upon re-aeration which increases mortality.

Quiescence and Escape Strategies

Rice plants adapt to submergence by two opposite strategies- the low oxygen quiescence strategy and the low oxygen escape respectively (Luo *et al.*, 2011) [27]. In the low - oxygen quiescence strategy, there is conservation of energy reserves, reduction in growth levels and a delay in energy crisis (Setter and Laureles, 1996; Sauter, 2000; Bailey-Serres and Voesenek, 2008) [49, 46, 5]. This strategy is beneficial particularly in deep floods. In contrast to quiescence strategy, the low – oxygen escape strategy is characterized by enhanced shoot elongation in plants for reaching the surface and restoration of air contact (Bailey-Serres and Voesenek, 2008) [5]. Unlike the low-oxygen quiescence strategy, this strategy is beneficial only in shallow floods. Under this strategy plants possess more aerenchyma tissues for efficient transportation of gas to below-ground parts where rate of oxygen is limited (Sauter, 2000; Voesenek *et al.*, 2003) [46, 54].

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Physiological Basis of Submergence Tolerance

Submergence tolerance is defined as “the ability of a rice plant to survive 10–14 days of complete submergence and renew its growth when the water subsides” (Catling, 1992) [9].

Aerenchyma formation

Rice is a semi-aquatic plant and it is well adapted to submergence due to the formation of aerenchyma tissue which facilitates aeration of submerged root. The induction and formation of aerenchyma occurs 24-72 hours after the application of anaerobic treatment. Greater aerenchyma tissues are found in plants grown in lowlands having excess water as compared to those plants grown in uplands under water deficit condition. Previous studies showed that the formation of aerenchyma tissues takes place in roots on short-term (7 days) exposure of rice to complete submergence and the process was faster in tolerant cultivars as compared to susceptible varieties.

Elongation ability

Limited elongation is the requirement for submergence tolerance in rice. Reduced elongation under complete submergence for 1-2 weeks is crucial for survival because when water recedes, lodging would likely to occur in the elongating plants. The genotype which possesses limited elongation ability during submergence is classified as ‘tolerant’ because for elongation, such a genotype uses only a small quantity of available carbohydrates leaving larger reserves for survival during submergence (Sarkar *et al.*, 1996) and resumption of growth when water levels recede (Das *et al.*, 2005) [15].

Relationship of plant hormones with underwater shoot elongation

The plant hormones - ethylene, gibberellin and abscisic acid (ABA) regulate shoot elongation in submerged plants (Kende *et al.*, 1998; Sauter 2000; Voeselek *et al.*, 2003) [24, 46, 54]. The gaseous hormone ‘ethylene’ triggers plant’s responses to submergence initially through physical entrapment. Under submerged conditions, ethylene plays a major role by regulating the positive and negative regulators of shoot elongation i.e., gibberellin and ABA, respectively. When ethylene concentration increases in plant tissues, there is a reduction in ABA level (Hoffmann-Benning and Kende 1992; Azuma *et al.*, 1995; van der Straeten *et al.*, 2001; Benschop *et al.*, 2005) [21, 4, 53, 7] with an increase in the level of endogenous gibberellin (Hoffmann-Benning and Kende 1992; Rijnders *et al.*, 1997; van der Straeten *et al.*, 2001) [21, 41, 53]. This results in increased shoot elongation during submergence (Kende *et al.*, 1998; Straeten *et al.*, 2003) [24, 55].

Submergence tolerance is associated with decreased ethylene level (Ella *et al.*, 2003) [16]. Since enhanced shoot elongation is not required for tolerance to complete submergence, blocking GA synthesis could lead to a reduction in elongation and energy conservation for maintenance and resurrection growth during and after submergence which results in enhanced survival. Shoot elongation is enhanced during submergence when GA is applied 48 h before flooding, and as a result, plant survival is reduced. Contrastingly, the elongation of shoot is enhanced by the application of inhibitor of GA biosynthesis- ‘paclobutrazol’ resulting in increased survival rate (Das *et al.*, 2005) [15].

Underwater photosynthesis and presence of leaf gas film

The gaseous exchange in plants is severely restricted by submergence due to the diffusion barrier by water. This

hampers the rate of photosynthesis and respiration resulting in mortality of plants upon submergence (Bailey-Serres and Voeselek, 2008) [5]. To improve underwater photosynthesis, internal aeration and survival rate, specific morphological and anatomical traits are utilized by rice plants (Mommer *et al.*, 2006; Colmer *et al.*, 2011) [33, 12]. When some terrestrial wetland plants are submerged under water, then they develop new ‘semi-aquatic’ thinner leaves having thinner cuticles and re-oriented chloroplast which helps in improving gas exchange and thereby underwater photosynthesis (Mommer *et al.*, 2004, 2005) [34, 35]. Some other wetland plants such as rice possess superhydrophobic leaf surfaces which retain a thin layer of gas on their leaves when submerged. The presence of these leaf gas films facilitates gas exchange by enlarging water-gas interface and hence improves underwater photosynthesis, internal aeration, sugar status and growth (Pedersen *et al.*, 2009) [39].

Leaf hydrophobicity

It is already known that rice leaves, when submerged, possess gas films on both the adaxial and abaxial surfaces and both the surfaces are equally hydrophobic in nature (Pedersen *et al.*, 2009) [39]. A comparative study between rice genotypes-Kinmaze and drp7 mutant based on leaf gas film retention when submerged as well as leaf surface hydrophobicity reveals that loss of leaf gas film is associated with loss of hydrophobicity of leaf surface because leaves of rice genotype-Kinmaze are hydrophobic and leaf gas film persists during submergence, whereas in drp7 mutant, leaf gas film was lost after 1 day of submergence and water droplets were not repelled from the leaves resulting in decreased hydrophobicity.

Chlorophyll Fluorescence Imaging

Environmental stresses including submergence cause damage to the photosynthetic apparatus especially photosystem II in plants. Photosystem II emits chlorophyll fluorescence and changes in this fluorescence provides information about the photosynthetic activity on all aspects. Chlorophyll fluorescence imaging can be used as an important tool to measure the responses of plants to various abiotic stresses including submergence. Chlorophyll fluorescence parameters like F_0 is defined as the minimum level of fluorescence when all the reaction centres are open, F_m is the maximum fluorescence level when a brief saturating pulse of light is applied to a dark adapted leaf when all the reaction centres are closed and the difference between F_0 and F_m is known as the variable fluorescence, F_v . According to Butler 1978 and Genty *et al.*, 1992, F_v/F_m ratio indicates the maximum quantum yield of PSII chemistry. The occurrence of any abiotic stress including submergence results in photoinhibition (Long *et al.*, 1994) and thereby causes a reduction in F_v/F_m . Under submergence, abiotic factors like light and oxygen becomes limiting in plants in comparison to unstressed conditions. Therefore, when plants are exposed to air, the photosynthetic apparatus gets affected severely. However, tolerant cultivars acclimatize to the new environment quickly but susceptible cultivars are unable to adjust with the prevailing conditions which is considered as one of the main reasons for decrease in the values of different chlorophyll fluorescence parameters (Panda *et al.*, 2008) [38].

Root Traits

Root health is of great significance for survival during submergence and recovery too. Previously, it was observed that the cultivars which are tolerant to submergence possess

comparatively healthier roots than that of intolerant landraces (Singh *et al.*, 2014) [52]. The presence of leaf gas film under submergence can enhance the carbohydrate supply and help in regeneration of adventitious roots, and improve the aeration of root and rhizosphere. Root porosity is an important trait for the growth of root in flooded soils and this can be determined by measuring the rate as well as extent of aerenchyma development so as to minimize the resistance to movement of O₂ down the root. Formation of effective barriers to radial oxygen loss (ROL) in rice helps in better aeration of active root tips and rhizosphere and also reduces the harmful effects of toxins in anoxic soils (Kirk *et al.*, 2014; Yamauchi *et al.*, 2018) [25, 59]. Colmer & Voesenek 2009 [10] reported the genetic variations in root porosity and ROL rates in rice. The genotypes which maintain healthier root systems during submergence can survive for a longer period of time and recover quickly when water level recedes.

Efforts should be made in future for exploring genetic variations in root as well as shoot traits in order to improve submergence tolerance in rice. Useful alleles for traits should be discovered so that survival during submergence and recovery after flooding can be accelerated.

Biochemical Basis of Submergence Tolerance

During complete submergence, the expression and activity of chlorophyllase enzyme that is responsible for chlorophyll degradation is enhanced due to an increase in ethylene synthesis (Das *et al.*, 2005; Ella *et al.*, 2003 and Sarkar *et al.*, 2001) [15, 16, 43]. Submergence results in protein degradation (Anupam *et al.*, 2017) [47]. Biochemical parameters like carbohydrate status before and during submergence is one of the most critical factors for tolerance. The overall growth of plants depends upon carbohydrate content (starch and soluble sugars). The mobilization of soluble sugars takes place from source to sink as the sources of energy throughout the life cycle of plants. Proper level of soluble sugars should be maintained after submergence for quick recovery and survival. During submergence period, old leaves are decayed and new leaves regenerate rapidly as soon as flood water recedes which leads to survival of plants (Bailey-Serres *et al.*, 2008 and Sarkar *et al.*, 2006) [5, 44]. Therefore, the availability of enough carbohydrate after submergence is required for fast recovery and plants survival. In rice genotypes possessing greater elongation ability, the storage carbohydrates deplete during submergence and hence energy reserves are exhausted whereas in rice cultivars showing less elongation ability during submergence, the carbohydrates are stored and used after the flood water recedes resulting in speedy recovery and higher survival rates in these rice varieties (Das *et al.*, 2005) [15].

Reactive oxygen species and antioxidative enzymes

The exposure of rice plants to submergence stress induces rapid accumulation of reactive oxygen species (ROS) such as superoxide (O₂⁻), hydrogen peroxide (H₂O₂), and hydroxyl radicals. They cause oxidative damage of lipids, proteins and nucleic acids and thereby disrupting normal metabolism ((McKersie and Leshem 1994) [31]. Plants have evolved several active oxygen scavenging systems which consist of both anti-oxidant enzymes and non-enzyme anti-oxidants to counteract the free radicals and hence reduce the damage caused due to oxidative stress and reactive oxygen species (Ismail *et al.*, 2010) [14]. Among them, superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR) and

dehydroascorbate reductase (DHAR) play major roles in protection of plants from the damage caused due to oxidative stress (Asada 1997) [2]. O₂⁻ is mainly scavenged by SOD through dismutisation of O₂⁻ into H₂O₂ (Bowler *et al.* 1992) [8]. Ascorbate peroxidase (APX), glutathione reductase (GR), catalase (CAT) and peroxidase (POX) are helpful in scavenging H₂O₂ (Asada 1997) [2]. CAT converts H₂O₂ to water and oxygen (Mates 2000) [30]. Besides its scavenging activity, POX is involved in lignification of cell walls (Waffenschmidt *et al.*, 1993) [56]. Ascorbate acts as a reducing substrate to detoxify H₂O₂ in plant cells (Mellhorn *et al.*, 1996 and Nakano *et al.*, 1987) [32, 36]. Glutathione reductase is involved in reduction of oxidized glutathione to the reduced glutathione (Noctor *et al.*, 2002) [37]. Antioxidants like ascorbate and glutathione scavenge H₂O₂ in synchrony with monodehydro ascorbate reductase (MDAR) and GR through which ascorbate is regenerated (Horemans *et al.*, 2000) [22]. High level of anti-oxidant enzymes helps plants to cope up with oxidative stress (Mandamanchi and Alschner 1991) [28]. Most of the studies have revealed that the level of anti-oxidant enzymes increases during submergence in rice plants. One of the possible reasons for increased enzymatic activity is absorption of molecular oxygen from the surrounding water.

Genes Related to Submergence Tolerance and Escape

Many reviews have already been presented regarding the characterization of genes that are responsible for submergence tolerance in rice. Quantitative trait locus (QTL) mapping shows that the submergence quiescence response is regulated by Submergence1 (SUB1) locus containing tandem-repeated group VII of ethylene responsive factor (ERF-VII) (Xu *et al.*, 2006) [58]. In contrast, the locus containing tandem-repeated ERF-VII genes, SNORKEL1 (SK1) and SNORKEL2 (SK2) regulate the escape response (Kawano *et al.*, 2009) [20]. SUB1QTL of indigenous landrace of rice, 'FR13A' developed from Odisha has been used as a source for breeding submergence tolerance in rice till date.

SUB1A Confers Submergence Tolerance to Rice

It has been reported that SUB1A gene which is limited to some *indica* and *aus* varieties of rice (Xu *et al.*, 2006 and Singh *et al.*, 2010) [58, 50] confers tolerance to complete submergence (Singh *et al.*, 2010; Fukao *et al.*, 2006 and Fukao *et al.*, 2008) [17, 50, 18]. In addition, the closely related submergence inducible genes-SUB1B and SUB1C are present in all rice accessions. SUB1A exists in two allelic forms - SUB1A-1 and SUB1A-2 in submergence tolerant and intolerant rice (*indica* and *aus*) accessions on the basis of nucleotide changes in the region that code for protein (Xu *et al.*, 2006) [58]. SUB1A-1 allele is present in tolerant accessions such as FR13A whereas SUB1A-2 is found in intolerant *indica* varieties. SUB1A-1 differs from SUB1A-2 in promoting rapid transcript induction by stress whereas SUB1A-2 promotes a lower level of transcript accumulation in response to submergence (Fukao *et al.*, 2006; Xu *et al.*, 2006) [17, 58]. During submergence, the synthesis and entrapment of ethylene is promoted, which enhances mRNA accumulation of SUB1A (Fukao *et al.*, 2006) [17]. Ultimately, SUB1A checks ethylene production along with the suppression of gibberellic acids (GA). SUB1A is responsible for increasing the levels of brassinosteroids, which, in turn, enhances degradation of GA that is biologically active (Schmitz *et al.*, 2013) [48]. Increased levels of brassinosteroids results in accumulation of a DELLA protein, 'SLENDER RICE1' (SLR1) that negatively regulates signaling of GA. Likewise, SUB1A, submergence induced

ethylene increases the abundance of SK mRNAs (Hattori *et al.*, 2009) [20]. SNORKEL genes promote accumulation of bioactive GA in internodes under submergence (Ayano *et al.*, 2014) [3]. Kende *et al.*, 1998 [24] and Fukao *et al.*, 2008 [18] recognized that in deep water rice, the internode elongation is triggered due to increased biosynthesis of GA by ethylene under submergence. In deep-water rice, endogenous ABA level decreases rapidly in response to submergence which leads to increased responsiveness to GA (Kende *et al.*, 1998) [24]. ABA degradation occurs when active form of ABA is hydroxylated to the unstable intermediate - 8'-hydroxy ABA in presence of ABA 8'-hydroxylase (ABA8ox), then it is spontaneously converted to phaseic acid (PA) (Cutler *et al.*, 1999) [13], which is further reduced to inactive dihydrophaseic acid (DPA).

Role of SUB1C gene in rice under submergence

SUB1C gene is also induced by ethylene while GA upregulates *SUB1C* expression but *SUB1A* suppresses the expression of *SUB1C*. *SUB1C* is associated with GA-mediated carbohydrate metabolism and the extent of underwater elongation in rice. Fukao *et al.*, 2006 [17] reported that *SUB1C* gene regulates the expression of α -amylase gene (*OsAmy3D*) in rice leaves under submergence. Interestingly, *SUB1C* gene has been expressed at higher level in submergence intolerant varieties of rice as compared to that of tolerant cultivars under submergence (Xu *et al.*, 2006) [58].

LGF-1 gene contributes to submergence tolerance

Besides the above mentioned genes, the remarkable discovery of *LGF-1* gene involved in leaf gas film formation and underwater photosynthesis (Kurokawa *et al.*, 2018) is an important step towards improvement in submergence tolerance in rice. It is observed that leaf hydrophobicity occurs due to the presence of various macro, micro and

nanostructures on leaf surfaces such as epicuticular waxes (Marmur, 2003; Koch and Barthlott, 2009) [29, 26]. The formation of abundant epicuticular wax which is important for leaf hydrophobicity and gas film retention on submerged leaves, involves a C30 primary alcohol, and *LGF-1* plays a vital role in controlling the synthesis of the primary alcohol. The discovery of *LGF-1* can provide us information about understanding the variation in leaf gas film retention among different rice genotypes (Winkel *et al.*, 2014) [57]. We can possibly identify alleles so that higher expression of *LGF-1* associated with epicuticular wax platelets abundance and duration of leaf gas film retention during submergence in rice could be conferred.

MAPK signaling cascade and submergence tolerance

MAPK (Mitogen Activated Protein kinase) signaling cascade is an evolutionarily conserved eukaryotic signal transduction module which transduces environmental and developmental signals (Rodriguez *et al.*, 2010) [42]. Sinha *et al.*, 2016 [51] proved that the interaction between *SUB1A* and MAPK cascade help rice plants to adapt to severe effects of submergence. It is known to us that one of the most important characteristics of *SUB1A*-mediated submergence tolerance is reduced shoot elongation upon submergence (Schmitz *et al.*, 2013) [48]. When pre-treatment using a specific MAPK inhibitor was given to rice genotypes namely Swarna and Swarna Sub1 before 1 day of submergence stress, no effect of pre-treatment was found in either variety in the absence of submergence (Sinha *et al.*, 2016) [51]. There was no variation in shoot elongation of MAPK-inhibitor pre-treated Swarna after submergence, whereas in Swarna Sub1 pretreated using the inhibitor, marked shoot elongation was observed leading to a decrease in the accumulation of *SLR1* and *SLRL1* transcripts, proving thereby that MAPK cascade is involved in *SUB1A*-mediated submergence tolerance in rice.

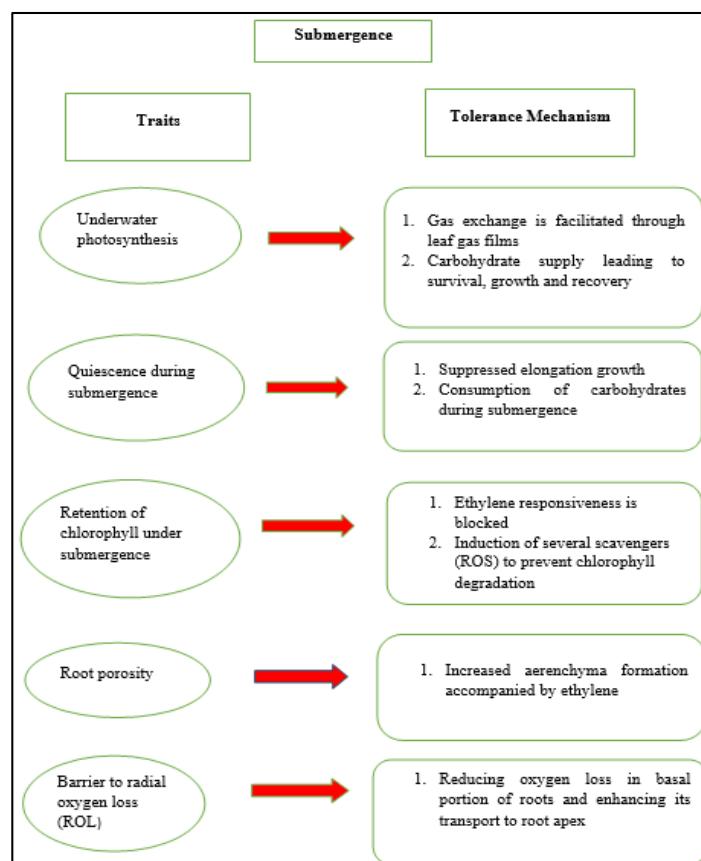


Fig 1: Traits and their respective mechanisms of submergence tolerance.

Conclusion

The present review provides the information about physiological, biochemical and molecular basis of submergence tolerance in rice. This article reviews the recent progress towards improvement in tolerance to submergence by discovery of LGF-1 gene that plays an important role in leaf gas film retention during submergence as well as epicuticular wax platelet abundance. In future, the influence of epicuticular wax platelets on leaf hydrophobicity can be studied among different rice genotypes. Many other traits whether physiological or biochemical or genetic are need to be explored for improving submergence tolerance in rice.

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