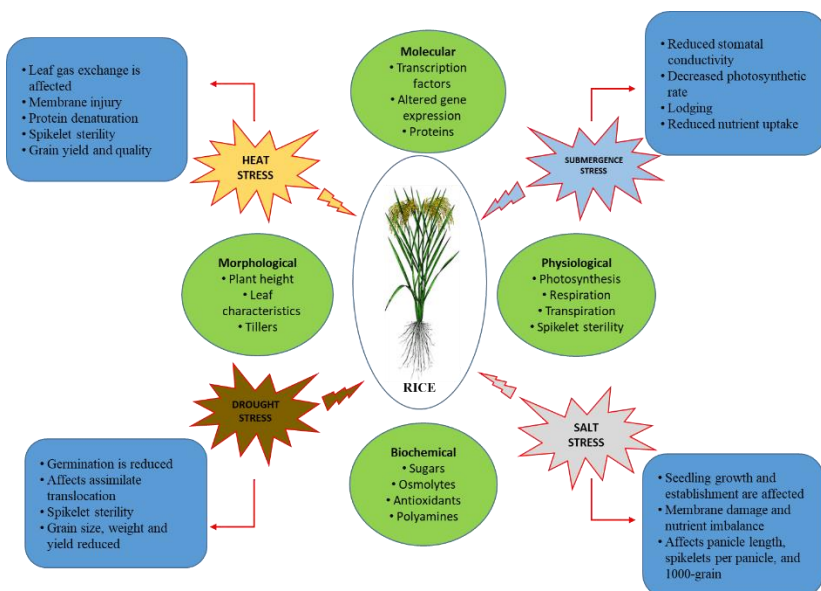# ABIOTIC STRESS PHYSIOLOGY OF RICE: AN UPDATED OVERVIEW IN THE ERA OF CLIMATE CHANGE

K Chakraborty*†, PS Hanjagi†, S Mondal, SM Awaji, MJ Baig and P Swain

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GRAPHICAL ABSTRACT

SUMMARY

Abiotic stresses pose a serious threat to rice production globally. Under the present climate change scenarios, the poor and marginal farmers particularly from rainfed agro-ecologies (rainfed upland, shallow lowland and lowland) are compelled to bear a frequentheavy toil due uncertain weather events. Among different abiotic stresses, rice crop is vulnerable to severe drought, excess water in terms of complete or partial submergence and anaerobic germination, salinity, high and low temperature, along with lowlight stresses. Identification of unique germplasm/ landraces and understanding the underlying tolerance mechanism in them is of immense importance in today's context. Characterization of these

unique genotypes for morpho-physiological and key molecular traits is required to identify secondary traits contributing to stress tolerance and enhanced yield under unfavourable growing conditions. Hence, identification of suitable donor and secondary/putative traits is the need of the hour to develop climate resilient rice cultivars.

1. INTRODUCTION

Past few decades' have drawn serious attention of researchers and policy-makers globally due to the vulnerability to climate change, influenced by natural disasters and hazards, along with threat to food insecurity. The mean surface air temperature of our planetis likely to increase by 1.8 to 4.0°C by 2100 due to anthropogenic activities contributing to climate change (IPCC, 2007).There is an increase in the average global temperature of land and ocean surface to the tune of 0.85°C during the period of 1880 and 2012, with a projected decadal increase of at least 0.2°C from now onward. Rice (*Oryza sativa* L.) is one of the important cereal crops of the world. It is a staple food for nearly 50% the world's population (Carriger and Vallee, 2007).In fact, the backbone of global food security is dependent on rice production in Asia, where 90% of the world's rice is produced and consumed under both irrigated and rainfed agro-ecosystems. Due to its wide geographic distribution extending from 50°N to 35°S, rice production is projected to be highly vulnerable to future climatic changes. Rice crop is sensitive to different abiotic stresses to a varying extent, which is likely to be exacerbated with climate change scenarios. Extreme weather events such as high temperatures coinciding with critical developmental stages, floods causing complete or partial submergence, soil salinization due to intrusion of seawater and most importantly unprecedented drought spells are highly detrimental for rice production, particularly in rainfed ecosystems.
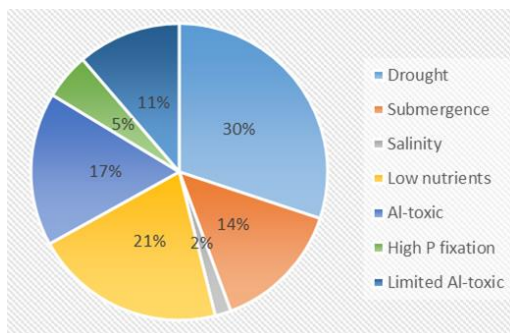

Fig. 1 Relative distribution of rice growing areas in Asia vulnerable to different abiotic stresses (*FAOSTAT 2013. Database available at http://faostat.fao.org/site/339/default.aspx.*)

The changing climatic conditions make the rice crop vulnerable to moderate to severe drought stress, germination stage oxygen deficiency (GSOD) or submergence stress depending upon the timing of the natural events, and increase in salinity level in coastal rice belts, lowlight stress situation due to heavy down pouring or prolonged cloudy weather conditions and heat stress due to increase in temperature during dry spells mostly in the grain filling stage. Frequent occurrence of such climatic extremities in many parts of the Indian subcontinent and other parts of globe have been indicated in recent reports. Secondary traits contributing towards tolerance to a particular stress or combination of stresses can help achieve yield improvements in such stressful environments. Land races with broad genetic bases and wider adaptability, combined with tolerance to various stresses serve as useful donors for different abiotic stress tolerance. Hence, in the present scenario, identification of suitable donor and secondary/putative traits for developing high yielding varieties through conventional or molecular approaches with an added advantage of understanding stress tolerance mechanism is of paramount importance. In this chapter, we have discussed recent advancements in(i) the impact of different abiotic stresses on growth and physiology of rice crop, (ii) the adaptive and tolerance response shown by rice to these abiotic stresses and (iii) the possible management options to combat against these stresses.
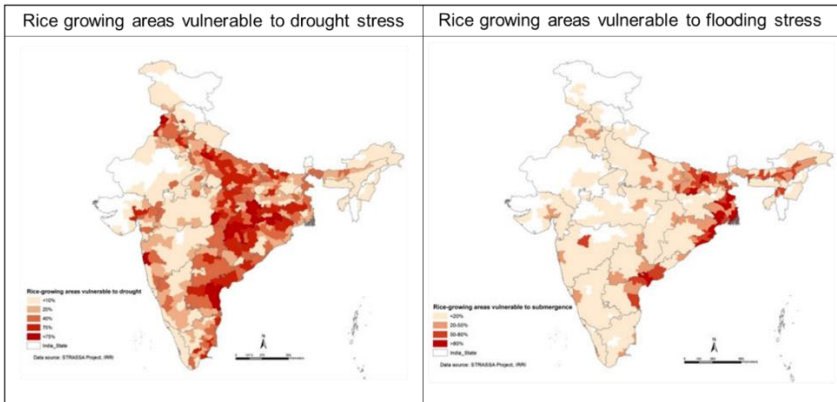
Source: STRASSA Project Report, IRRI

Fig. 2 Vulnerability map of rainfed rice growing areas of India to drought and flooding stress.

2. IMPACT OF DIFFERENT ABIOTIC STRESSES IN RICE PRODUCTION AND PHYSIOLOGY

Grown under diverse range of ecosystems, rice production is prone to different environmental stresses like drought, salinity, submergence, cold as well as high temperature and lowlight. With changing climate, rice cultivation especially in the rain-fed ecology (rainfed upland, shallow lowland and lowland) is facing multi-faceted problems. The common cellular disorders caused by various abiotic stresses and common plant responses counteracting adverse effects of these abiotic stresses are given in Fig.3.
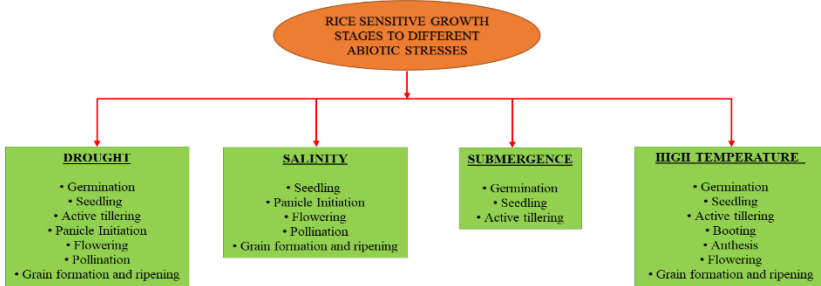

Fig.3 Sensitivity of rice crop to different abiotic stresses at different growth stages.

2.1. Drought

Rice is very much susceptible to soil moisture stress during the reproductive stage, resulting in a significant reduction in grain yield (Palanog et al., 2014). Drought stress related symptoms appear in plants when the root cells experience a scarcity of water or when the overall leaf transpiration rate is very high compared to the normal conditions. Drought stress severely hamper the growth and developmental process, which ultimately leads to loss in production/ yield. The magnitude of yield loss depends on several factors, among them growth stage of rice and duration of stress are two important factors for deciding severity of drought stress. Severe drought stress at the vegetative stage can cause up to 20% yield loss while a mild drought stress at the flowering stage in rice resulted 28% yield loss (Kumar et al., 2014). Severe drought stress at flowering stage recorded a yield loss ranging from 53-92% (Lafitte et al., 2004; Lafitte et al., 2007). Rainfed rice growing regions of Eastern India experience moderate to severe drought irregularities during the south-west monsoon. With >17 million hectares of rainfed areas, Eastern India and few adjoining regions of Nepal are considered the largest drought-affected region in Asia (Huke and Huke, 1997). In order to improve water uptake, plants under drought stress divert assimilates towards the

roots thereby disturbing the assimilates balance (Leport et al., 2006). Earlier reports showed that, the rate of photosynthesis and the sucrose concentration in leaves regulates the export of assimilates from source to sink (Komor, 2000). Drought stress affects the overall process of carbon dioxide fixation (photosynthesis) and hampers the net production of sucrose. Net amount of sucrose that has been produced in photosynthetic cells decreases, which eventually hamper the overall process of exportation from source (leaf) to sink (root or seed) (Kim et al., 2000), thereby limiting the net productivity of the plant. To meet the present and future global food security identification of drought-resistant crops that have been adopted to growth under dry weather conditions and also able to maintain a constant production(Barnabas et al., 2008).

2.2. Submergence

Among several different kinds of environmental constraints, flash flooding or submergence stress, particularly in low-lying rice growing ecologies is one of the major catastrophic event that detrimentally affects plant survival and crop yield. Globally, complete submergence due to flooding and associated loss is most prevalent in the low-lying rice growing areas of the world. It was reported that out of the 22-million-hectareof rice crop affected by flash flooding, half of which is in Eastern India (Dar et al., 2017). Although rice is a water loving crop and requires a considerable amount of water for their normal growth and development, the over-abundance of water in case of submergence or waterlogging is destructive for rice. Globally, water stagnation due to floods was the reason for almost 66% of all harm and misfortunes to crops during the period of 2006 and 2016, with an estimated loss in billions of dollars (FAO, 2017).

Submergence is a form of flooding stress. It is further be differentiated into two types- complete submergence and partial submergence. In the case of complete submergence, entire plant canopy is fully dipped inside water for 1-2 weeks, whereas, in case of partial submergence, a portion of plant canopy or shoot terminal is present above the water level. Broadly, plants employ two different strategies to cope up with the anoxia that arises due to submerged conditions. The first is known as quiescence or low-oxygen quiescence syndrome, where plants exhibit a limited growth and elongation during the submergence stress (Colmer and Voesenek 2009) and the second is an escape strategy, also called low-oxygen escape syndrome, where the plants show faster elongation of internode to come out of water as quickly as possible (Bailey-Serres and Voesenek 2009). In quiescence strategy, plants store their carbohydrate reserve by restricting their inter-nodal growth. However, the plants remain alive under submergence and resume its growth by utilizing the energy from the reserved starch once the standing water recedes (Colmer and Voesenek 2009).

2.3. Waterlogging or Stagnant Flooding

Based on the depth of the water, soil flooding can be classified in two different categories- submergence and waterlogging. Waterlogging or stagnant flooding stress is defined as a condition, where a part of the plant canopy remains under water for a prolonged period of time. Setter and Water (2003) reported that waterlogging substantially limits the rates of exchange of oxygen and other gases in different parts of plants. Therefore, the movement of oxygen from the air to different submerged portions of plant tissues (Lee et al., 2011) are hampered, creating an abnormal situation for the plant, which is popularly known as hypoxia (less than<21% O_2in water) (Sasidharan et al., 2017). In case of stagnant flooding the diffusivity of oxygen in water is approximately 10,000 times slower compared to the rate present in air. Similarly, the flux of O_2 into soils is approximately 320,000 times less compared to normal soil, as instead of gases, here, water fills the pores that are present in soil (Colmer and Flowers 2008). Therefore, it is said that the prime factor that is present behind waterlogging stress is slow diffusion of oxygen in the different portions of plants. The low availability of O_2under waterlogging is further amplified/ extended by the rapid consumption of it by the soil born microorganisms. Reports showed that, in some cases, O_2 deficiency responses in soil occurs within a few hours of waterlogging. In addition to the O_2 deficiency, Setter et al. (2009) showed that the stress responses further facilitated the production of toxic substances such as Fe^{2+}, Mn^{2+} and H_2S by reduction of redox potential and causes severe damage to plants under waterlogged conditions. Hence, growth and development of almost all cultivated crop is severely affected by waterlogging stress. Rice being adapted to semi-aquatic ecology is reported to have a comparatively less effects of prolonged flooding stress leading to partial submergence of plant canopy, however enough genotypic variation in waterlogging tolerance is found in rice (Nishiuchi et al., 2012).

2.4. Germination Stage Oxygen Deficiency

Submergence or soil flooding during the process of germination imposes germination stage oxygen deficiency (GSOD). The problem of GSOD is of immense importance in rain-fed ecologies and direct seeded rice, where sudden heavy rainfall just after direct sowing of rice creates a havoc in germination, seedling emergence and initial crop establishment. Few rice genotypes have developed a unique adaptive mechanism to germinate and extend its coleoptile (shoot portion) under water by sacrificing normal growth of the coleorhiza, even under complete anoxic condition (Magneschi and Perata 2009) – a phenomenon popularly known as GSOD or anaerobic germination (AG) (Ray et al., 2016). It has been reported that, in general, rice coleoptile which is present under water can elongate at the rate of 1 mm h^{-1} to reach the atmosphere or emerge out of from the water level. At cellular level, it is facilitated by the rapid elongation of basal

cells (up to 200 μm in 12 h), immediately after emerging from embryo (Narsai et al., 2015). Though rice has adaptations to grow under different aquatic habitat, its anaerobic germination potential (AGP) or survival ability varies greatly among different rice genotypes and landraces, which ultimately provide an edge/platform to a few genotypes that perform better under oxygen deficient conditions over others. There are a few rice genotypes which can efficiently cope with the hypoxic/anoxic conditions in case of complete submergence of the seeds just after sowing (Vijayan et al., 2018).

2.5. Salinity

Soil salinization/ alkalization is a world-wide problem for the agriculture, affecting nearly 6% of total Earth's land, as a result of natural accumulation and deposition over long periods of time. Besides, secondary salinization in agricultural soils occurs due to improper agricultural activities. Based on the global reports, 2% of all dry land is becoming salinized, and more than 20% of irrigated soils are affected. Faulty irrigation practices, due the use of poor-quality irrigation water containing substantial amounts of dissolved sodium chloride or other neutral salts increase the soil salinity (Tester and Davenport 2003). In general, rice genotypes show considerable variability for salt-tolerance. Rice is classified as a salt sensitive crop with a threshold salinity tolerance level of only 3 dS m^{-1}.Wide genotypic variation in salinity responsiveness was reported among different species of rice and their wild relatives (Menguer et al., 2017).Rice crop is reported to be relatively tolerant to salinity stress during germination, active tillering and towards maturity, but sensitive during early seedling and reproductive stages, where an additional concentration of as little as 50 mM NaCl to the soil can reduce rice yield significantly (Zeng et al., 2003). In General, salinity stress is associated with two different types of stresses on plants: initially it creates an osmotic stress, later it is accompanied by ionic stress. The genetic basis behind tolerance to osmotic stress has been poorly investigated and majority of work in the field of salinity is focused to identify the genetic basis of tolerance that is associated to ionic stress (Roy et al., 2014). Research findings indicate that members of *Indica* are good Na^+ excluders and K^+ maintainers, absorb high amounts of K^+ in cells, therefore, able to maintains a low Na^+/K^+ratio in the shoot portion (Lee et al., 2003).

2.6. High Temperature

The impact of heat stress on rice grain quality and quantity depends on the stage of crop development. Heat stress in rice affects the anthesis and grain filling stages. Even one-degree rise in temperature above the optimum temperature results in 7-10% yield loss in rice (Fahad et al., 2017). Exposure of rice plant to 41°C for 4 hours at flowering stage causes irreversible damage resulting in

complete spikelet sterility. During the months of April and May in Eastern India, due to early sunrise, temperatures rise above 35ºC during anthesis affecting pollination in rice. The post-anthesis warming at night time has adverse effects on leaf net photosynthesis and increased night respiration rates. Heat- induced spikelet sterility at flowering reduced the grain yield. Temperatures above a critical point of 35 °C at the flowering time inhibited anther dehiscence, resulted lower pollen shed on a stigma, and leading to incomplete fertilization (Jagadish et al., 2010). Under heat stress, due to increased rate of transpiration, water loss is more during day time, which eventually affecting certain important physiological processes in plants. Furthermore, studies identified that a continuous exposure to heat stress decreases the mass and growth of roots, also hampers the water and nutrient transportation process in different parts of plants (Wahid et al., 2007; Huang et al., 2012).

2.7. Lowlight

Light is the immense source of energy and also an important environmental factor for plant growth, development and metabolism that regulates photosynthesis process and photo-morphogenesis (Müller-Xing et al., 2014; Zhu et al., 2017). However, plants frequently get exposed to different intensities of light like excess-light (EL) or low light (LL), causing stress to plants. These stressful conditions exert negative impacts on photosynthetic activity and eventually hamper the plant growth and yield (Nishiyama and Murata 2014). It has been reported that different intensities of light significantly hampered several physiological and metabolic processes including photosynthesis, antioxidant production and carbon nitrogen fixation, which ultimately affect different important agronomic traits of plants. (Apel and Hirt 2004; Wang et al., 2013). Despite several reports of negative effects of light stress on plant growth and development, light stress is the one of the most uncharacterized and less studied abiotic stresses in plants. However, there is a recent increase in advocacy for deciphering the significance of light stress and how EL and low light (LL) affect plants development (Banerjee and Roy Choudhury 2016; Zhu et al. 2017).

The low incidence of solar radiation coupled with fluctuating light during the wet season is one of the major constraints for realizing the low productivity in Eastern and North-Eastern India. Light being a crucial factor for the plant development, stress experienced by the plants under low irradiance results in an increased leaf length andwidth, increased leaf area, increased time period for growth, decreased differentiation of panicle and reduced grain yield (Murchie et al., 2005). Lower rates of photosynthesis (due to low irradiance per unit leaf area) is accompanied by the reduction in the thickness of mesophyll and number of cells/mm^2 in leaves. But surprisingly the total chlorophyll content,especially chlorophyll-bwas higher under low light. Low light stress

negatively influences the stomatal conductance. The decreased rubisco activity accompanied by subsequent increase in the intracellular carbon dioxide concentrations is also observed under low light intensity.

3. ADAPTIVE AND TOLERANCE MECHANISM OF RICE TO DIFFERENT ABIOTIC STRESSES

3.1. Drought

Propensity of the plant to grow, develop and produce a good economic yield under water stress is referred to as drought tolerance (Nezhadahmadi et al 2013). Tolerance to drought in plants are maintained by complex traits, which is a combined function of various morphological, biochemical and molecular characters. To facilitate the selection or development of drought tolerant rice varieties, screening of different rice genotypes is necessary, along with this, further understanding of the various mechanisms that govern the yield of rice under water stress. Plants generally utilize several mechanisms to withstand drought stress, which are categorized as the escape, avoidance, or tolerance response to drought stress. Escape is a classical adaptive mechanism that characterized by a state of dormancy or necrosis caused by programmed death of cellular tissues, with the exception of those that are required for regeneration or regrowth upon a change of season or alleviation of stress such as renewal of available water after prolonged drought conditions.
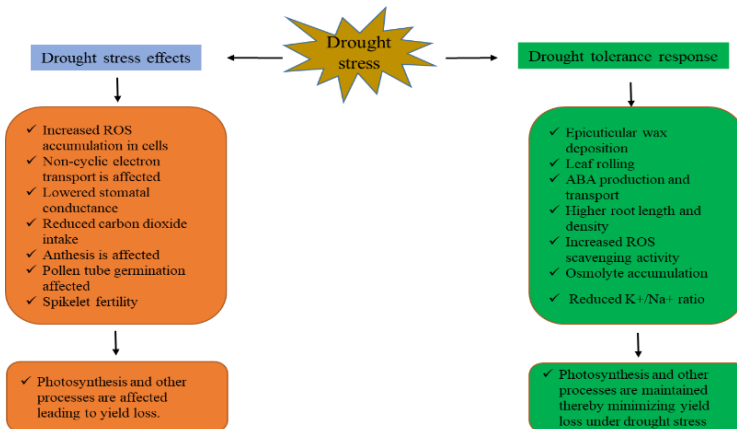

Fig. 4 Effects of drought stress on rice and physiological responses to cope up with the stress.

Similarly, drought avoidance is an adaptive strategy of rice, that involves a group of mechanisms including deep rooting or leaf curling to prevent cellular dehydration process under drought stress. Several morphological parameters play important role in maintenance of turgor, initiation of leaf rolling, induction of epicuticular wax deposition on the leaf surface, deep and coarse root with greater xylem vessel radii and lower axial resistance to water flux are indicators of drought stress tolerance. Besides, stomatal function or exchange, photosynthesis, photosystem activity, net chlorophyll content and translocation of solutes from source to sink is also important for a prolonged period of drought stress. Photosynthetic ability has been regarded as important indicator of the growth of plants, because of their direct link to net productivity. Drought causes not only a substantial damage to photosynthetic pigments, but it also leads to deterioration of thylakoid membranes. Chlorophyll pigment played important role in photosynthesis, and chlorophyll stability index, which is a measure of integrity of membrane of the pigments found to correlate with drought tolerance. Apart from metabolic processes, hormonal activity under drought stress is also important. Previous studies involving ABA showed that ABA act as a signalling molecule, and an efficient ABA signalling contributes to drought tolerance. In addition, at molecular level a large number of genes in rice are up- or down-regulated by drought stress, which not only enhances the plant survival in drought conditions but also improves the crop productivity.

3.2. Submergence

Among the cultivated plants, rice is the most efficient crop which is capable of surviving under complete submergence for a considerable period of time. There are different mechanisms to cope up with submergence stress. In case of complete submergence, reduced growth and elongation or in short quiescence under submergence was found to be an efficient strategy to withstand complete submergence stress. Only few rice genotypes processing a *SUB1* QTL in their genomecan follow this process. Reduced elongation of internode under flash flood condition (complete submergence for 1-2 weeks) is crucial for survival as the elongating plants often tend to lodge as soon as the water subsides (Vergera et al. 2014). Therefore, elongation of internodes under submergence can be crucial for identifying susceptible/ tolerance rice lines. Also, as elongation of internodes is an energy dependent process, rate of starch degradation was also decisive for identifying tolerance. Also, content of non-structural carbohydrates, which is important for providing energy and for the maintenance of key metabolic processes in cells, before and after submergence is important for determining susceptible and tolerant genotypes. Besides, this is also important for regeneration and recovery of seedlings after the water recedes (Sarkar, 1998; Das et al., 2001). Underwater, maintenance of chloroplast integrity is another vital factor for plant survival. Rapid change in chlorophyll fluorescence traits were

also observed in sensitive genotypes under submergence stress. Thus, chlorophyll fluorescence (ChlF) traits could be a possible selection criteria for identification of submergence tolerance genotypes in rice (Panda et al., 2007& 2008).
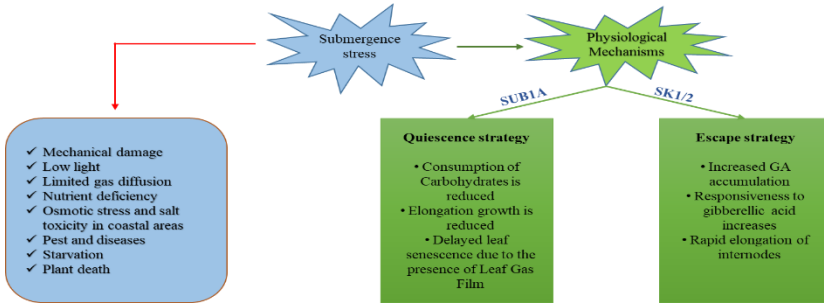

Fig. 5 Effects of submergence on rice physiology and tolerance mechanisms.

Besides these well studied adaptive and/or tolerance strategies, amount of leaf gas film thickness that is present in the surfaces of rice leaves is also important to decide plant survival under stress. It is also beneficial for rice and helps to exchange gases, when plants are dipped into water (Pedersen et al., 2009). Among many cereal leaves studied for the presence of such leaf gas film in adaxial and abaxial leaf surfaces, rice was found to possess the most thicker leaf gas film, which may well be associated with its unique ability to withstand complete submergence for fairly long period of time among all the cereal crops. Recently, Chakraborty et al. (2021) showed that thickness of these leaf gas films were influenced by the presence of active *SUB1* gene in the rice genetic background.

The higher in-built activities of antioxidant enzymes in tolerant cultivars are reported to be an useful physiological adaptation strategy to hypoxic condition. It is beneficial and helpful to maintain the functionality of the enzymes under hypoxic/ anoxic condition. A mechanistic understanding of molecular regulation underlying submergence tolerance and escape survival of plants has been studied through functional validation and characterization of key genes, that are responsible for acclimation to submergence stress in rice. Modified ethylene signalling through *SUB1* gene action imparts submergence tolerance. Submergence stress facilitates the biosynthesis and entrapment of ethylene in tissues, which stimulates the induction of *SUB1A-1*gene and promotes its synthesis. Later, *SUB1A* activity limits the plant elongation process *via* suppression of ethylene production in feed-back inhibition manner, which finally blocks the production of gibberellic acids and checked the overall elongation process of internodes under submergence.

3.3. Waterlogging or Stagnant Flooding

Aerenchyma formation is a basic phenomenon of lowland rice and also an important adaptive strategy to withstand stagnant flooding, which allows unhindered transport of O_2 from well-aerated shoots to submerged roots (Jackson and Armstrong 1999). Along with the formation of aerenchyma, low-land rice showed a limited diffusion of O_2 from root apex. This process was facilitated by forming a specialized barrier like structure on the root that popularly known as barrier to radial O_2 loss (ROL). This specialized structure was helpful to minimize the overall O_2 loss from root apex to the surrounding environment. Furthermore, this specialized structure or barrier is also helpful to check the movement of soil-derived toxins (i.e., reduced metal ions) and gases (e.g. methane, CO_2, and ethylene) into the roots (Greenway et al., 2006) that are inimical for the root cell. It has been reported that, this trait was associated with both upland and lowland rice species and helpful to withstand waterlogging conditions (Colmer, 2003b).

Stagnant flooding may last for several months, where O_2 deficiency causes severe energy depletion in plants. In general, rice plants escape from the flooding to survive under semi-deep or deep water-flood conditions. To achieve this, deep-water rice rapidly and substantially elongate their internodes to avoid complete immersion of plant canopy in water. Remarkably, some deep-water rice cultivars can increase their height by up to 25 cm/day (Vergara et al., 1976). This rapid elongation allows the leaf tips to extend above the water surface and enable the rice plants to efficiently photosynthesize and exchange gases for respiration (Bailey-Serres and Voesenek 2008).The process of elongation was regulated by different activities of hormones. Among different hormones, ethylene plays a master regulator role in elongation. Initially, ethylene biosynthesis is activated, and accumulates in cells, later, accumulated ethylene further regulates the production of GA and ABA content. As internode elongation is promoted by GA or repressed by ABA, the overall GA/ABA ratio in cell is important to regulate the process of elongation (Kende et al., 1998; Sauter, 2000). Based on the reports of Steffens et al. (2011) aerenchyma formation in different tissues was enhanced by a gaseous hormone, ethylene. Additionally, Hattori et al. (2009) identified two important candidate genes *SNORKEL1* (*SK1*) and *SNORKEL2* (*SK2*) that are responsible for internode elongation and present in deep-water rice. Introgression of*SK1* or *SK2*in non-deep-water rice showed enhanced growth of internodes, and validated that the *SK* gene members are the key players behind escape strategy of rice under deep-water.

3.4. Germination Stage Oxygen Deficiency

Anaerobic mode of respiration usually yields much less energy as compared to the aerobic mode of respiration. As normal electron transport process, including energy production (ATP) was hampered due to scarcity of oxygen, in case of anaerobic germination the energy requirement is largely fulfilled by glycolysis followed by alcoholic gate of fermentation (Guglielminetti et al., 1995, 2001; Hwang et al., 1999). Based on the transcriptomic data, it was observed that, under anaerobic mode of germination, starch and glucose metabolism enzymes related genes are majorly up-regulated (Lasanthi-Kudahettige et al., 2007; Hussain et al., 2016; Narsai et al., 2017). Therefore, based on these reports, it is predicted that, activity and up-regulation of the enzymes related to starch degradation is crucial for identifying susceptibility and tolerance. Previous reports showed that, starch degrading enzymes like α-amylase, aldolase and sucrose synthase are up-regulated in GSOD and specifically in case of tolerant cultivars. Susceptible plants are unable to up-regulate these enzymes and die due to scarcity of energy. (Ismail et al., 2009; Miro and Ismail 2013). It was also reported that a higher *RAmy 3D* gene expression (Ismail et al. 2009; Takahashi et al. 2014) as well as greater up-regulation of rice cytosolic hexokinase (*OsHXK7*;Kim et al 2016) was observed in case of GSOD stress. Similar study by Kretzschmar et al. (2015) identified a major gene *OsTPP7* that is related to trehalose breakdown pathway, which helps to maintain a balance between trehalose and starch, therefore, starch breakdown process and energy production was not hampered in case of GSOD stress. Mapping QTLs imparting high anaerobic germination potential (AGP) has been initiated (Angaji et al., 2010; Baltazar et al., 2014; Kretzschmar et al., 2015) and one of the identified QTL, *qAG-9-2* has been fine-mapped to identify*OsTPP7* gene, which encodes trehalose-6-phosphate phosphatase that are involved in starch mobilization process during germination (Kretzschmar et al., 2015).Recent studies showed effective operation of anaerobic respiration and nitrogen metabolism in tolerant rice genotypes which led to more energy efficient metabolic system under oxygen limiting GSOD condition, and resulted in better ROS handling and cellular pH maintenance (Vijayan et al., 2018).

3.5. Salinity

Under salinity stress, initially osmotic stress becomes more predominant whereas with time when more and more salts are absorbed, ionic effect plays the leading role. Therefore, salt stress creates a cumulative response of both osmotic and ionic stress and adaptation to both is required to combat salt stress (Reddy et al., 2017). With time injury symptoms due to salinity are visible, susceptible cultivars die early compared to tolerant cultivars in a salty environment (Singh et al., 2014, Pradhan et al., 2019). To deal with this adversity, plants generally restrict the movements of ions such Na^+ or Cl^- ions to the growing meristematic tissues and

young photosynthetic organs that are crucial for plant survival. Tolerant rice cultivars like Pokkali either absorbs low levels of Na^+ or restricts the movement of Na^+ to the photosynthetically active portions in comparison to K^+ and thereby maintains low $Na^+{:}K^+$ ratio in shoot / leaf, and protects the vital tissues (Yeo & Flowers 1984; Yeo et al., 1990; Cuin et al., 2011; Singh & Sarkar 2014;Kobayashi et al., 2017). High Na^+ in the cell cytoplasm impairs several physiological and biochemical courses of action (Chen et al., 2014; Silva et al., 2015; Bendaly et al., 2016), which restricts plant growth. Recently, Chakraborty et al. (2020) showed that a combination of both ion exclusion and tissue tolerance strategies can effectively balance the salt-tolerance strategies in rice, which could potentially minimize the energy cost of salt-tolerance.
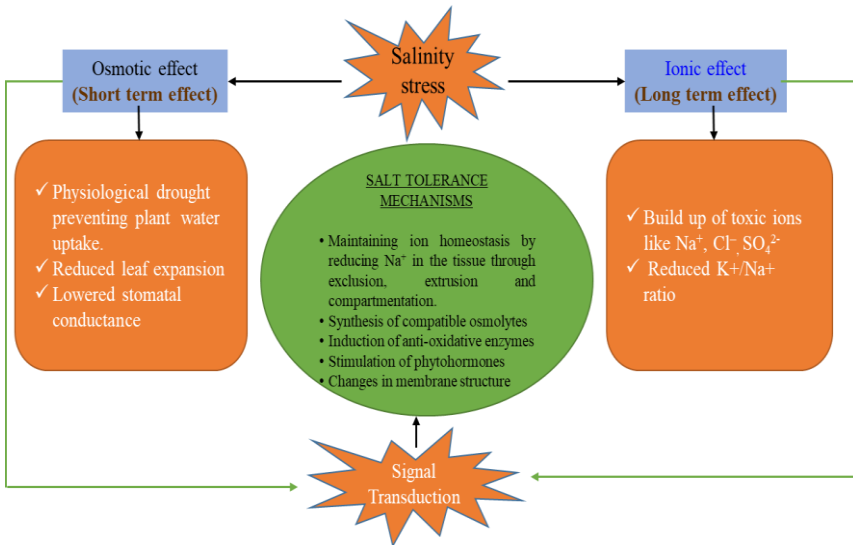

Fig. 6 Effects of salinity in rice plants and tolerance mechanisms.

Molecular studies of the transporters showed that different group of transporters are involved in reducing overall Na^+ accumulation in shoots and their subcellular compartmentalization in the vacuoles. Among them, the high affinity potassium transporter (HKT), salt overly sensitive (SOS) and Na^+/H^+ Exchanger (NHX) gene families are the key players for salinity tolerance and important to maintain the cellular homeostasis (Mickelbart et al., 2015). HKT members are important for maintaining the overall tissue concentration of Na^+ and K^+. *OsHKT1;5* was identified as the functional gene of *Saltol* QTL, the major quantitative trait locus (QTL) for salt accumulation in *O. sativa* genotypes (Ren

et al., 2005). Reports showed that, *OsHKT1;5* is a plasma membrane localized Na^+/K^+ channel that allows selective transport of potassium to the upper portion of cells. It effectively efflux Na^+ from the xylem and transport it to adjacent parenchyma cells, therefore minimizing the upper flow of Na^+ (Hauser and Horie 2010).Robust screening effort including several *O. sativa* cultivars, landraces and *O. glaberrima* (AA genome) genotypes showed that overall concentration of sodium in leaf blades is a determining factor to identify susceptibility/ tolerance.*OsHKT1;5* gene was identified as a major determinant for tolerance at early vegetative stage; the more active the efflux transporter, the more tolerance was maintained by the plant, which directs the Na^+ exclusion from the transpiration stream and less amount of Na^+ is translocated to leaves (Platten et al., 2013). The scenario was quite complex in case of reproductive stage. Recently, Chakraborty et al. (2019) showed that selective transport of K^+ over Na^+ is an important factor for governing reproductive stage salt tolerance in rice. Besides, overall tissue sodium concentration in flag leaves is also important and crucial for deciding susceptibility and tolerance at reproductive stage. Different Na^+, $K^+$and proton transporters of the family SOS, NHX, HKT, V-ATPase and V-PPase was found to be important here and its over-expression ultimately decides the plant fate in case of reproductive stage salt tolerance.

3.6. High Temperature

Rice is highly sensitive to heat stress particularly at flowering and post-flowering stages. Exposure to short periods of heat stress coinciding with flowering has resulted in significant yield losses reported in India, China and Japan. During anthesis heat stress leads to irreversible reduction in spikelet fertility, mainly by affecting sensitive physiological processes such as anther dehiscence, pollination, and early fertilization events. To minimize heat stress related damage, plants generally adopt three mechanisms viz., heat escape, heat avoidance and heat tolerance. Heat escape generally deals with time of day of flowering, especially early morning flowering, heat avoidance strategy mainly applies transpiration cooling process for maintaining a convenient canopy temperature and heat tolerance strategy generally deals with resilient reproductive processes (Jagadish et al., 2010). Based on the reports, early –morning flowering genotypes which showed a better anther dehiscence and flower opening ability at a cooler time of day are preferably more desirable candidates for heat tolerance and heat escape (Satake and Yoshida 1978). Later, Jumiatun et al. (2016) showed that rice cultivars those are able to maintain a low leaf temperature and well-exerted panicle under high temperature, possibly perform better under high temperature stress.
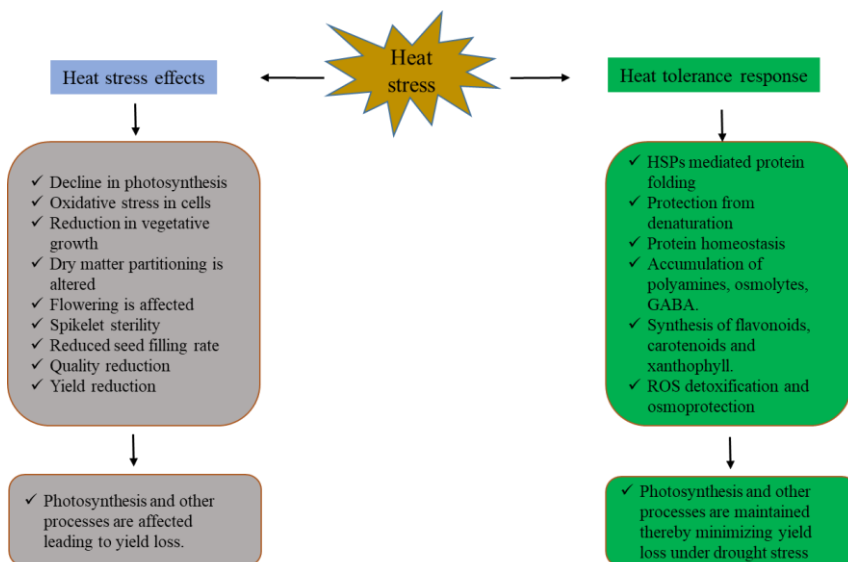
Fig. 7 Effects of heat stress on rice and physiological responses to cope up with the stress.

Apart from the heat resistance mechanisms, to limit the excess heat generation process in leaves, several plants maintain a thick cuticular wall out of the leaf surfaces that limits excess absorption of solar radiation. Altering leaf orientation under changing temperature by turning the leaf blades away from light and change their orientation by rolling in such a way that they seem to be parallel with falling sun rays thereby protecting leaves from heat stress (Hasanuzzaman et al., 2013). High temperature stress tolerant plants maintain homeostasis by physiological alterations like osmolyte accumulation resulting in increased water uptake and retention in the cell and stomatal regulation, and enhanced photosynthesis. Morphological alterations like reduced cell size, closure of stomata, greater xylem vessels and leaf rolling are also impart adaptations to heat stress tolerance. Biochemical alterations like reduced generation of reactive oxygen species due to enhanced antioxidants (SOD, CAT, POD), activity and modifications in membrane by increasing unsaturated fatty acids alters membrane fluidity under temperature stress to re-establish homeostasis, and to protect and repair damaged proteins and membranes (Vinocur and Altman 2005). At molecular level, upregulation of stress responsive genes, changes in proteomics, transcriptomics and metabolomics have shown to impart tolerance to heat stress. At cell level, activity of ion transporters, LEA family proteins, production of osmolytes, antioxidant defense related enzyme activities, and transcriptional

control of the genes that involved in this processes are essentially required to neutralize the stress effects (Rodríguez et al., 2005). Significant genotypic variation has been documented in rice for heat stress induced spikelet sterility (Khan et al., 2019).

Nowadays, combined effect of drought and heat is a common type of abiotic stress that negatively affects production in rice. Combined drought and heat stress during flowering and grain filling affect both yield and quality of the produce. Stress occurring at flowering stage affects yield and its components more significantly while combined stress during grain filling had a stronger negative impact on quality, primarily chalkiness of the grain. Combined stress during grain filling had significant impact on the overall chalkiness or the proportion of grains with >75% chalk compared with flowering stage stress. Combined drought and heat stress during flowering resulted in the reduction of plant height and biomass.

3.7. Lowlight Stress

The exhaustive research carried out to understand the mechanisms of lowlight tolerance in rice exhibited two kinds of mechanism when they encounter low light (LL) stress such as (i) shade avoidance and (ii) shade tolerance. Primarily the phytochrome photoreceptors sense the reduction in the R:FR ratio, which may occur either due to the neighbouring vegetation, actual shade, future shade or reduced PAR, and induce a suite of traits to grow towards the light. Collectively this is known as shade avoidance response (SAS). Shade tolerance is exhibited by species from forest understories that cannot outgrow the surrounding trees and adopt tolerance responses (Gommers et al., 2012). The various physiological and morphological characteristics of plants to withstand lowlight are depicted in Fig. 8.
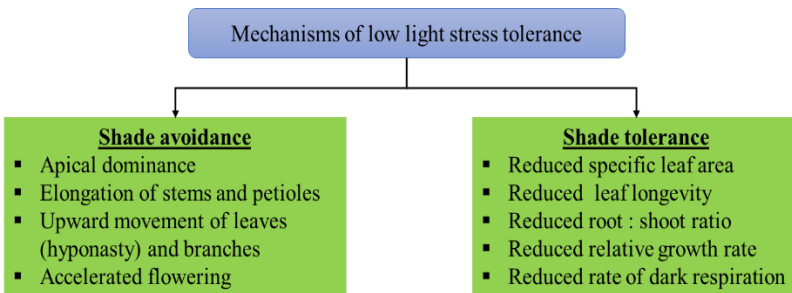

Fig. 8 Mechanisms of low light stress tolerance in rice.

4. OMICS APPROACHES IN UNDERSTANDING ABIOTIC STRESS TOLERANCE IN RICE

'Omics', the modern-day scientific buzz word can be defined as the sciences of evaluating the functions of different biological information and their interaction in different clusters of life. It encompasses the studies at the gene level such as genomics and epigenomics;mRNA or transcript level such as transcriptomics; at functional protein level known as proteomics or may be at the metabolite level known as metabolomics and lipidomics or may the interactions (interactomics) and phenotype (phenomics) level (Langridge and Fleury 2011). The Fig. 9 summarizes the different omics-based approaches for deciphering abiotic stress tolerance mechanisms in rice plants.
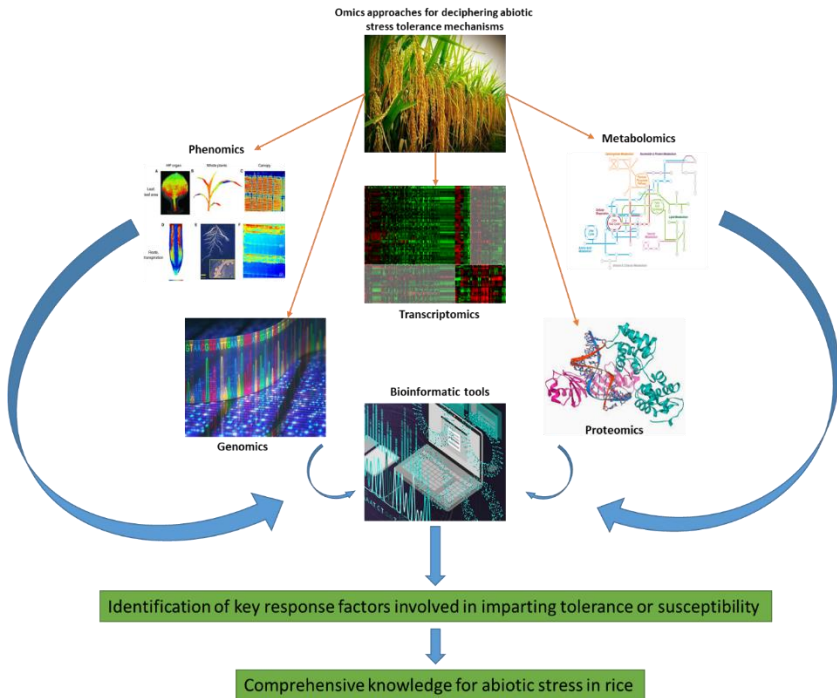

Fig. 9 Omics-based approaches for deciphering abiotic stress tolerance mechanisms in rice plants.

Omics approaches are inter-dependent and overlapping. The amalgamation of the huge data generated through omics approaches is very much

important to derive a logical conclusion to ascertain the major cell or tissue specific response-cascades differing in two or more experimental conditions arising out of abiotic stress tolerance studies. Genomic studies can give an overall view of the most dominant responsive genes in tolerant varieties. The expression pattern and the complex networks of mRNAs which have an important role in the functioning of tolerant varieties under stress conditions are revealed through transcriptomics. Discovery of the major proteins participating in the defence systems of rice plants can be done with help of a key approach called proteomics (Zou et al., 2011). Metabolomics exhibitions crucial secondary metabolites of tolerant varieties for combating abiotic stress. Phenomics approaches are helpful to understand the relation between phenotypic traits and genomic data. Bioinformatics tools integrate all the data obtained from the "omics" sciences and leads to the accumulation of comprehensive knowledge about tolerance mechanisms to abiotic stresses in rice.

5. POSSIBLE STRATEGIES FOR IMPROVING ABIOTIC STRESS TOLERANCE IN RICE

In order to successfully combat the adverse effect of abiotic stresses, both genetic improvement and agronomic/ physiological management strategies are important. The development of drought-tolerant varieties will greatly enhance and stabilize rice productivity in drought-prone areas. Introgression of yield QTLs *qDTY1.1*, *qDTY2.1* and *qDTY3.1* that are effective under drought stress into genetic background of popular rice varieties helps in mitigating yield losses due to drought stress. Breeding for plants with less root length density in shallow layers of soil, and high root length density in medium- and deep-layers, has been considered an efficient water management strategy (Wasson et al., 2012). Application of P (50% more than the recommended dose), Fe (30 kg ha-1), and Si (200 kg ha^{-1}) under water deficit stress condition resulted in a significant increase in grain yield by 7, 9, and 12%, respectively (Kumar et al., 2019). Application of Silicon improves the spikelet number, spikelet fertility, and grain weight and enhances yield.

Similarly, introgression of Saltol QTL and *SKC1* (*OsHKT1;5*) through gene pyramiding had yielded considerable success in developing salinity tolerant rice cultivars. Now, breeders are trying to combine *SUB1* and *Saltol* QTLs in the same genomic background of rice for increasing the tolerance to multiple abiotic stresses like salinity and submergence. Genetic variability could be utilized to screen for abiotic stress tolerant genotypes and could be utilized for developing tolerant and well-adapted rice cultivars. Genotypic variation exists in rice cultivars for anthesis time. Early flowering could be considered as an escape mechanism for avoiding elevated temperature stress (Julia et al., 2012). Early

morning flowering is a useful trait that could be used to reduce spikelet sterility by advancing the time of flowering in the early morning when the air temperature is cooler (Yoshida et al., 1981). Adopting a late or early maturing cultivar is one of the approaches to escape high temperature during grain filling (Ohe et al., 2007, Krishnan et al., 2011). Growth regulators can also be employed to minimize adverse effects of heat stress in rice. The foliar application of salicylic acid (0.1 mM) induced high-temperature tolerance and ameliorated the effect of heat stress in rice (Chandrakala et al., 2013). Some growth regulators, such as methyl jasmonate, which advances the flowering time to early morning, could be used to mitigate heat stress (Kobayasi et al., 2009). The application of $CaCl_2$ (10 mM) was shown to ameliorate the heat stress-induced reduction in gas exchange, PSII efficiency, photosynthetic water use efficiency, spikelet fertility, and leaf chlorophyll content in rice (Chandrakala et al., 2013). Screening and identification of genotypes for higher non-structural carbohydrate pool, higher biomass and stable photosynthesis under high temperature could serve as genetic donors for reducing temperature-induced yield loss.

5. CONCLUSION

Harvesting the higher production with minimum loss under abiotic stress situation is essential the context of climate change scenarios, and it is a challenge for the researchers to understand the adaptive mechanism and tailor rice genotypes for optimum performance from limited resources. The rainfed rice cultivation in the country is highly affected by the effects of climate change. To combat the stress, it is essential to integrate crop physiology, molecular genetics and breeding approaches to dissect complex abiotic stress tolerance traits, and develop the next generation crops which can withstand the adverse climate and ensure food security. The popular high yielding rice varieties should be stacked with multiple stress tolerant gene(s)/QTLs for making them climate resilient. Thus, mega varieties with multiple tolerant genes for submergence, anaerobic germination, yield QTLs under drought and seed dormancy need to be stacked to make them truly climate resilient.

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