



Traditional rice cultivars grown in Hirakud dam reservoir: Source of submergence tolerance gene under waterlogged environments

Pramod Kumar Suna and Ekamber Kariali[‡]

School of Life Sciences, Sambalpur University, Jyotivihar, Sambalpur-768019, Odisha, India.

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ABSTRACT

In view of the recent climate change scenario which is responsible for creation of multitude of abiotic stresses, development of stress tolerant/resistant crop genotypes is of immense significance for sustainable crop production under stress-prone ecosystems. Submergence or waterlogging is such a harmful abiotic stress factor which can have an adverse influence on rice crop throughout the growing season leading to severe yield losses to the farmers. Hirakud dam reservoir is a man-made water body where water accumulates during the rainy season leading to submergence which is unsuitable for cultivation of any crop and making large land masses unproductive. However, the local farmers live in the embankment areas of the dam reservoir cultivate a large number of submergence tolerant traditional rice varieties exhibiting a lot of variations in their stress resistance mechanisms. Though a huge diversity of traditional rice varieties are cultivated in the dam reservoir, no systematic study on identification of submergence tolerant genes have been carried out. Thus, a proper scientific investigation on this rice diversity will definitely be helpful in providing a source of rich gene pool to develop submergence-tolerant rice genotypes for exploitation of large water bodies for sustainable rice cultivation and making them agro-ecologically productive.

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1. Introduction

Rice (*Oryza sativa* L.) is the staplefood for more than half of the World population (Zhao *et al.*, 2017; Jang *et al.*, 2023) sustaining life in many developing and underdeveloped Nations across the Globe. In Asian countries, rice cultivation provides employment to majority of the people for maintenance of their livelihood. Most of the rice eaters live in low-income countries of the Asia where more than 76% of caloric intake was obtained from rice only (Panigrahi *et al.*, 2021). Before early 1960s, only traditional tall rice varieties were cultivated in almost all countries of the World where yield was very low and often unable to meet the food demands of human beings leading to hunger and starvation. In order to increase the yield potential of the plant, people used nitrogenous fertilizers. However, the result was not promising because the plants became excessively tall in response to nitrogenous fertilizers and lodged on the ground causing poor grain filling and reduction in grain yield.

Further, the poor yield in the traditional rice varieties was attributable to utilisation of most of the photosynthates for the growth and development of vegetative structures like stem, leaves and roots and very little fraction of photo-assimilates were partitioned into the grains. In the subsequent time of investigation for increasing the grain yield, rice breeders especially at the International Rice Research Institute, Philippines introduced some dwarfing genes in the tall *indica* varieties and became successful in developing the first ever semi-dwarf high yielding miracle rice variety 'IR-8' during early 1960s. This was possible because of the translocation of photosynthates to the grains at the cost of vegetative structures as the plant height was significantly reduced leading to improved harvest index. Subsequently, several IR-8 parented rice varieties were developed through traditional breeding and distributed among the farmers of developing and underdeveloped countries of the World for cultivation in their own farms leading to a quantum jump increase in rice production.

[‡] Corresponding author; Email: ekamberk@rediffmail.com/ekamberk@suniv.ac.in

Though grain production during 1960s was significantly increased, rice production has almost stagnated during the last 2-3 decades and farm yield seldom gone beyond 10 t ha⁻¹ (Panigrahi *et al.*, 2021) and thus failed to provide food security in many developing countries as there was a significant increase in population growth. Currently speculation is ripe for a severe shortage of food grains in near future which may bring starvation due to lack of another quantum jump in rice yield potential (Panigrahi *et al.*, 2021). Hence, in order to feed all the mouths of the burgeoning population, attempts are to be made to find out new yield thresholds and in this regard, huge biodiversity of traditional submergence-tolerant rice varieties grown in the embankment areas of Hirakud dam reservoir may provide a rich source of gene pool for their introgression into high yielding rice genotypes for exploitation of water resources under waterlogged environments for making those are a agro-ecologically productive and also for enhancement of farmer's income.

2. Hirakud dam reservoir as the habitat of submergence tolerant rice cultivars

Hirakud dam is the longest earthen dam in the World built over the river Mahanadi at Hirakud and is located in Sambalpur district of Odisha, India having latitude 21.32N and longitude 83.52E. The dam reservoir is a multi-purpose artificial water body constructed just after India's independence which covers a large land area both in Odisha and Chhattisgarh. Huge water accumulation over the soil surface in the embankment areas occurs during the rainy season which makes the habitat unsuitable for cultivation of any crop including high yielding rice. However, the farmers living in the embankment areas of the dam reservoir cultivate some traditional rice cultivars under such waterlogged conditions since long time. (Figure 1) These varieties are tall in stature and are highly tolerant to submergence and stagnant flooding. The dam reservoir area remains almost dry during the summer season and following the first rain fall, farmers sow the seeds just after ploughing the land before the onset of monsoon. Subsequently seed germinates after the first rain and vegetative growth of the seedlings is quite good because the reservoir soil is highly fertile due to deposition of silt, minerals and other organic matters carried through small rivers and streams during the previous rainy season. At the onset of rainy season, heavy rainfall causes excessive accumulation of water in the dam reservoir and some of the rice varieties rapidly elongate their stem internodes and leaf sheaths to keep some of the leaves above the water level to carry out normal photosynthesis especially during the vegetative growth phase, so that photo-assimilates are synthesized in the leaves which help in the

survival of the plant. The photosynthates act as the source of energy to combat against the submergence-induced stress for plant survival. This mechanism of resistance to flooding stress is known as 'escape strategy' (Bashar *et al.*, 2019). Submergence-induced internodal elongation is also called 'floating ability' and is mostly evoked by the plant hormone ethylene (Kende *et al.*, 1998). Apart from stress escape strategy, some rice cultivars survive completely being submerged for longer time even for over a month. These varieties continue to grow luxuriantly well after the water level recedes and this strategy of flooding resistance is called 'quiescence strategy' (Oe *et al.*, 2022). In such situations, plants experience hypoxia or anoxia stress because of restriction in diffusion of oxygen into the lower parts of the plant that are completely under water (Mondal *et al.*, 2020; Mital *et al.*, 2022). Increase in plant height and water depth in the natural habitats of the Hirakud dam reservoir for the four rice genotypes studied during the wet season of 2017 is presented in Fig.1

3. Waterlogged environments in dam reservoir: Stressful habitats for rice

Water logging or flooding is the third most vital abiotic constraints for crop production after heat and drought (Oladosu *et al.*, 2020) and rice is one among the most flood-threatened crop. About 30% of the marginal farmers and poor people live in the flood-prone areas of South Asian countries including India, Nepal and Bangladesh. In Indian situation, 5.2 million hectares of land areas are affected by occasional flood, out of the total 16.1 million hectares of rice growing areas and about 700 million people live in flood-prone rice cultivating areas of South Asia (Oladosu *et al.*, 2020; Jang *et al.*, 2023). More than 35% rice cultivable areas especially in African and Asian countries are prone to flooding stress where food insecurity is a major issue (Bailey-Serres *et al.*, 2012). In fact, flooding is a major constraint that threatens the human livelihood as it has tremendous influence on the vulnerability and poverty in the marginalised rural population of Africa and Asia.

The stressful habitats created through water logging or submergence is often developmental stage specific. Submergence during seed germination called anaerobic germination provides an anoxic or hypoxic environment causing low or poor germination and poor crop establishment or even death of the entire seedlings due to reduction in ATP production for maintenance of metabolic activities. On the other hand, if it is a fully grown submerged plant, it may lodge on the water surface after the flood subsides and may die eventually due to depletion of reserve carbohydrates and cellular energy (Oladosu *et al.*, 2020) leading to hindrance of growth and development. Rainwater flooding



Figure 1 : Rice cultivation in Hirakud dam reservoir.

is generally clear water which causes less crop damage than muddy and silted water as the latter becomes turbid and largely inhibit the entry of light into the submerged leaves leading to poor photosynthesis and has a considerable impact on the physiological status of the plant. Moreover, continuous water logging for longer duration causes chlorophyll and protein degradation, decrease of Rubisco activity and damage to photosynthetic apparatus leading to drastic impairment of photosynthesis (Panda *et al.*, 2008). Both oxygen deprivation and low solar intensity under prolonged water-logged situation are responsible for poor plant survival due to failure in new leaf production and severe damage of the older leaves. In addition to this, submerged plants produce a varieties of reactive oxygen species (ROS) such as hydrogen peroxide, hydroxyl radical, superoxide anion and superoxide radical which have severe damage potential to the cellular organisation leading to death of the entire plant. However, several rice plants grown in the Hirakud dam reservoir have tremendous potentiality for detoxification of such ROS in their natural habitats (data not shown). Under complete submergence, rice plants tend to elongate the stem internodes quickly in response to high ethylene production and oxygen deprivation. However, re-oxygenation after a period of oxygen deprivation, ethanol produced from glycolysis-derived pyruvic acid through anaerobic respiration (alcohol fermentation) is being trapped

in the plant tissue and subsequently converted to acetaldehyde which is responsible for severe post-anoxic cell damage (Voeselek *et al.*, 2013; Oladosu *et al.*, 2020). Generally, one glucose molecule can produce approximately 2 ATPs under anaerobic respiration whereas 38 ATPs are produced from the single glucose molecule during aerobic respiration and therefore plants under complete submergence face an acute problem of energy shortage because of very quicker consumption of the respiratory substrates like glucose and other simple carbohydrates (Lee *et al.*, 2019) leading to starvation.

4. Varietal diversity of submergence-tolerant rice cultivars in the dam reservoir

There was a huge diversity of traditional rice cultivars grown in the embankment region of Hirakud dam reservoir. However, the diversity has been lost at present due to discontinuation of cultivation of these varieties by the farmers as their grain yield is very low and also shortage of water occurs especially during the harvest period. Many cultivars grow upright as water level is high, but lodge by bending their stem internodes, if water level is decreased leading to death of the whole plant. Construction of many barrages on the upstream of river Mahanadi is also one of the principal reasons for problem in water accumulation in the rice growing regions especially during post-rainy

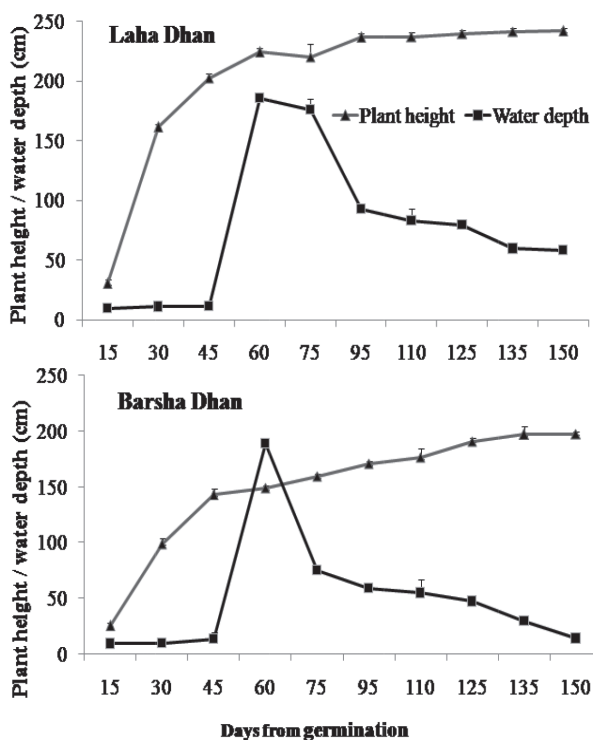


Figure 2: Plant height (triangle) and water level (square) in the natural habitats of Hirakud dam reservoir for the submergence escape rice cultivar *LahaDhan* (upper panel) and submergence quiescence rice cultivar *BarshaDhan* grown during the wet season of 2017. Vertical bars represent \pm SD values (n=3).

seasons at the time of crop harvest. As a result of water shortage, the upper part of the stem becomes weaker and lodge on water surface leading to poor grain filling for which there is significant yield loss. In spite of this, many farmers in the villages like Chikili, Gudam, Sardha, Kankel, Remta, Lora, Bhadrपाली, Ganthipali and many others located in the embankment regions of dam reservoir both in Odisha and Chhattisgarh still cultivate some rice varieties popularly known as *Budi dhan*. Out of these, varieties like *Laha dhan*, *Laha dumber*, *Lahagayanti*, etc. have been collected which follows escape strategy for submergence tolerance whereas *Barsadhan*, *Budi dhan*, *Hatipanjer*, *Khudiadhan*, *Radhajugal* etc. exhibit 'Quiescence strategy' of submergence tolerance.

5. Ethylene as the key controller of submergence tolerance in rice

Although the rice crop needs huge quantities of water for successful growth and development, exposure to continuous waterlogged conditions for long time is highly detrimental to the plant as the roots have to face the submergence-induced anoxia. However, several traditional rice cultivars are being cultivated in the upstream of the reservoir where the plants are subjected to continuous

submergence for longer period. Many cultivars utilise their food reserves like carbohydrates for the purpose of stem elongation by sacrificing few leaves at the basal region of the plant and keep some leaves above the water surface to carry out normal photosynthesis. (Figure-2) Some of the rice varieties can elongate their stem up to 20 cm per day. Plant hormone ethylene plays the key role resulting into spindly plants which can easily lodge on water surface when water level recedes leading to poor survival and producing little or no grain yield. However, these genotypes are important in lowland submerged areas where flood water does not recede for longer time and hence plant produces a good grain yield. Additionally, several genes related to escaping the submergence stress are expressed in these plants and plant hormones like ethylene, GA and ABA play pivotal role in their expression. Under deep water situation, ethylene accumulation promotes the expression of *SNORKEL* (*SK*) genes like *SK1* and *SK2* (Hattori *et al.*, 2009) through the activation of AP2/ERF transcription factors which are responsible for stem elongation due to activation of GA signalling pathways and down-regulation of Brassinosteroid (*BR*) biosynthesis genes (Bashar *et al.*, 2019) (Pathway I). However, *SK* genes are not expressed in all rice varieties and the expression is restricted to lowland deep water accessions only for stem elongation (Bashar *et al.*, 2019). In the second pathway, ethylene induced ERF transcription factors also enhances the expression of *Sub1* gene responsible for over accumulation of *Slender Rice-1* (*SLR1*) and *SLR1-Like-1* (GA signalling repressors) genes leading to reduction in GA accumulation and inhibition in leaf sheath and internode elongation and thus adopting 'Quiescence strategy'. (Figure-3) So, ethylene is the key factor responsible for induction of GA repressor genes and offset of GA signalling pathway where *Sub1* mediates the entire pathway resulting into inhibition of stem internode elongation in the Quiescence strategy (Fukao *et al.*, 2006). In addition to the ethylene induced AP2/ERF mediated expression of *SK* genes for controlling submergence escape, ethylene can also induce the expression of *OsEIL1a* (*Ethylene Insensitive 3-like 1a*) under submergence stress which binds to the promoter of *SK1/SK2* genes leading to accumulation of *SK1/SK2* transcript and is responsible for down-regulation of BRs and activation of GA (mainly GA1) signalling for rapid intermodal elongation for plant survival under escape strategy (Fukao *et al.*, 2012; Seo *et al.*, 2006) (Pathway III). Accumulation of GA1 activates the expression of cyclin genes which causes rapid cell division for elongation of the stem internode in lotus (*Nelumbonucifera*) for adoption of escape strategy (Wang *et al.*, 2018) and such mechanisms may also exist in rice. Apart from *Snorkel*-dependent internode elongation, *Snorkel*-independent stem elongation for escape strategy during submergence is basically mediated



Sampling of Deep-water rice from Hirakud dam reservoir

by ethylene-induced *OsEIL1a*, a protein which binds to the promoter of another gene called *SD1* (*Semi-dwarf1*) that functions independently of *Snorkel* and promotes the synthesis of bioactive GA especially GA4 leading to more rapid stem elongation for submergence escape (Kuroha *et al.*, 2018). Generally, the SD1 protein is responsible for the biosynthesis of bioactive GA like GA4 in addition to GA1 after submergence and GA4 is more efficient in stem elongation than that of GA1. Hence *Snorkel*-independent stem elongation mediated by SD1 is relatively faster in comparison to *Snorkel*-dependent pathway (Bashar *et al.*, 2019) for escaping the stress effects of submergence.

A number of research works revealed that, submergence tolerance of many rice genotypes are also mediated by the expression of a major QTL called ‘*Submergence1*’ (*Sub1*) present in the 9th chromosome of rice which encodes an ethylene response factor (ERF) and is responsible for restriction of stem elongation under submergence and thus adopt quiescence strategy. This *Sub1* QTL contains three genes such as *Sub1A*, *Sub1B* and *Sub1C* and this QTL has been isolated and characterised initially from a traditional rice land race *FR13A* grown in coastal Odisha in India (Xu *et al.*, 2006). Out of these three genes, *Sub1A* is mainly associated with submergence tolerance in rice because *Sub1B* and *Sub1C* are also expressed in the rice varieties which are not tolerant to submergence stress. Under complete submergence, prominent up-regulation of ethylene response factor (ERF) transcription factor genes like *ERF66* and *ERF67* occurs in presence of SUB1A-1 as suggested by Lin *et al.* (2019). In fact, SUB1A-1 is classified as Group-VII ethylene responsive factor (ERFVII) family and confers submergence tolerance through ‘quiescence strategy’ mediated by repression of ethylene and GA induced stem elongation (Lin *et al.*, 2023). So ethylene is indirectly responsible for repression of GA signalling and reduction of GA-mediated gene expression under submergence stress in a SUB1A-1 dependent manner. It is suggested that two

ERFVII genes like *ERF66* and *ERF67* are transcriptionally activated by SUB1A-1 and a regulatory complex is formed consisting of SUB1A-1 and ERF66/ERF67 for the activation of some downstream genes in rice to obtain submergence tolerance (Lin *et al.*, 2019; Lin *et al.*, 2023). It is also proposed that the 186th serine of SUB1A-1 protein is phosphorylated by a mitogen activated protein kinase 3 (MAPK3) in order to enable the SUB1A-1 for activation of downstream signalling genes to achieve submergence tolerance. Though most of the submergence sensitive rice plants possess SUB1A-2, another allele of SUB1A-1 where 186th serine is replaced by proline and this replacement drastically reduces the ability of MAPK3 to phosphorylate the SUB1A-2 protein leading to poor/no submergence tolerance ability. However, the contrasting ability of SUB1A-1 and SUB1A-2 based on MAPK3 mediated phosphorylation on submergence tolerance is yet to be identified (Lin *et al.*, 2023). During this investigation in Hirakud dam reservoir, many rice cultivars having the unusual ability for survival under complete submergence for a period of 25-30 days are available. Though carbohydrates act as the major energy reserves for plant survival, the possibility of up-regulation/ down-regulation of many other novel stress resistant genes might be involved in different metabolic pathways which needs to be investigated further.

6. Exploitation of rice cultivars for genetic manipulation towards yield enhancement

After the ‘Green revolution’, the miracle rice variety ‘IR-8’ was released from International Rice Research Institute, Philippines and subsequently the breeding efforts led to the generation of several IR-8 parented semi-dwarf high yielding rice varieties. The cultivation of such high yielding rice varieties has been highly popularised in most of the rice growing Nations of the World because of tremendous increase in their grain yield potential in comparison to the tall traditional rice cultivars which were grown traditionally by the farmers since time immemorial. Though the high yielding rice cultivars produce more grain yield, they are highly sensitive to most of the abiotic stresses including submergence or water logging and fail to sustain under extreme environmental conditions. But the traditional rice cultivars grown in the Hirakud dam reservoir in the natural ecosystems for ages are being exposed to multitude of both biotic and abiotic stresses and thus acquire a higher degree of resistance towards such extreme environmental stress factors. This resistance trait especially for submergence condition is not only expressed in the phenotype of the plant, but also in the genotype. Several such valuable genes have been identified in the submergence tolerant rice plants by many researchers.

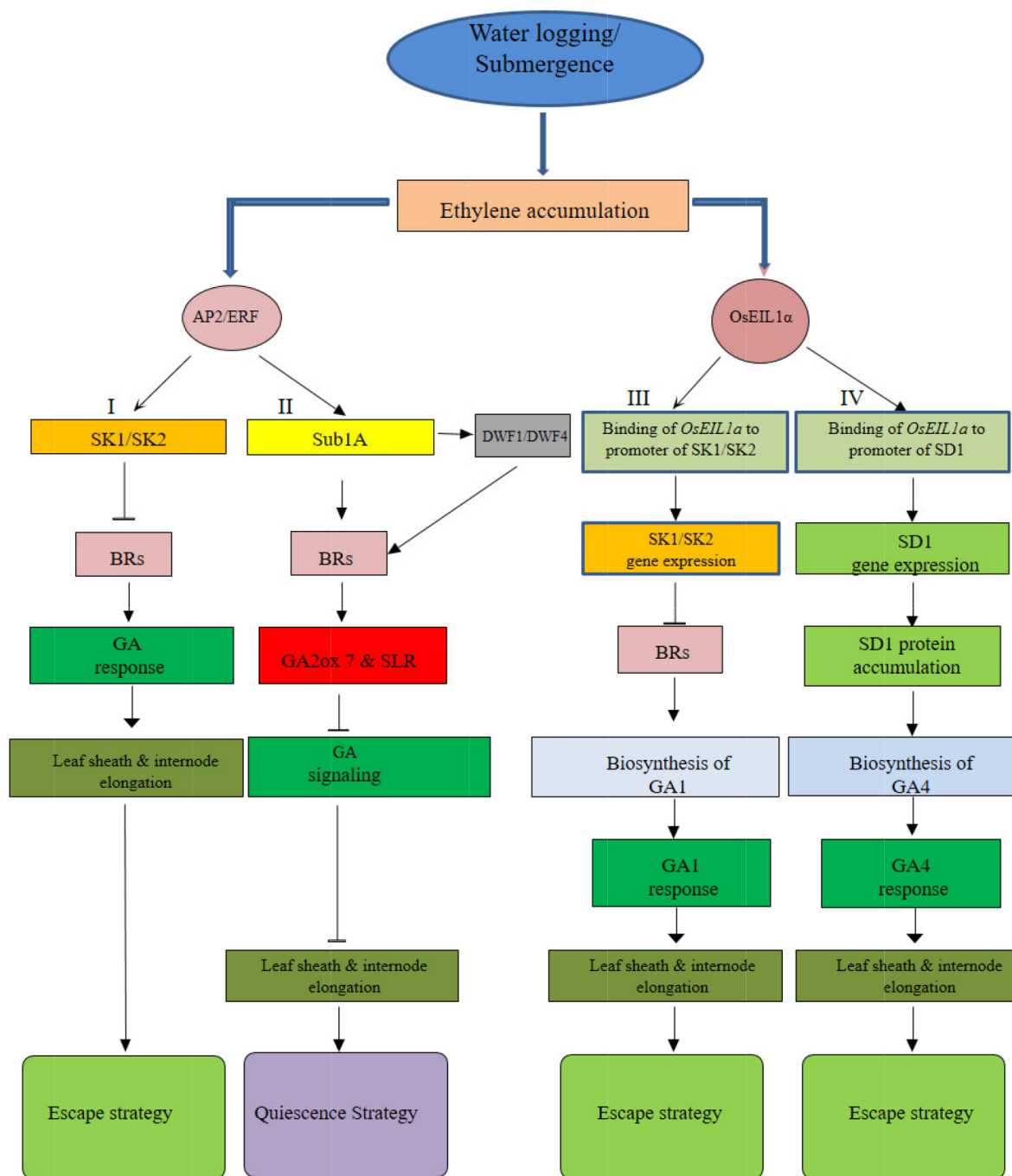


Figure 3: Ethylene mediated submergence tolerance describing one Quiescence and three escape pathways in deep water rice cultivars.

7. Conclusion

Identification and characterisation of stress resistant genes under various abiotic stresses in important crop plants like rice is one of the principal fields of research in present-day context to obtain yield stability under inclement weather conditions. Research efforts in this regard will definitely be of great help in introgression of novel stress resistant genes

into the high-yielding rice cultivars for production of stress tolerant high-yielding rice genotypes. Though the embankment areas of Hirakud dam reservoir exhibits huge diversity of submergence-tolerant traditional rice varieties, lack of systematic investigation for identification of stress resistant genes precludes their introgression into high yielding rice genotypes for successful cultivation under submerged/flooded environments. Development of

submergence tolerant high-yielding rice genotypes and their successful cultivation would be highly beneficial for exploitation of larger water resources for rice cultivation and increase of farmer's income. Thus, identification of novel submergence tolerant genes from the traditional rice varieties grown in the Hirakud dam reservoir is of high significance for increased rice grain yield and may be largely helpful for providing food security to the ever-increasing human population and also for a solution to World's food problem in future.

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