J.Natn.Sci.Foundation Sri Lanka 2023 51 (3): 533 - 546
DOI: http://dx.doi.org/10.4038/jnsfsr.v51i3.11333

RESEARCH ARTICLE

Agriculture

Submergence tolerance and tolerance mechanism: A study on traditional and improved rice genotypes at the seedling stage under complete submergence stress in Sri Lanka

HAPA Shyamalee and AL Ranawake*
Department of Agricultural Biology, Faculty of Agriculture, University of Ruhuna, Mapalana, Kamburupitiya, Sri Lanka.

Submitted: 03 August 2022; Revised: 27 March 2023; Accepted: 28 April 2023

Abstract: Submergence-tolerant genotypes in rice are essential for flood-prone lands, and recent studies have focused on dissecting tolerance mechanisms considering morphological and physiological changes in the plants upon submergence. Thirty improved rice varieties and sixty-two traditional rice accessions were screened for submergence tolerance under complete 9-day and 14-day submergence stress at the two-week-old seedling stage. The submergence tolerance level of each rice genotype was evaluated according to IRRI guidelines based on survival rates. Accordingly, rice genotypes were categorized into four groups: tolerant, moderately tolerant, moderately susceptible, and highly susceptible. Two Mawee accessions (3704, 3618) were submergence tolerant at 14-day submergence stress. The traditional rice accessions Ratawee3466, Mawee (8552, 4145), and Heenati4935 and improved rice varieties Bw400 were moderately submergence tolerant at 14-day submergence stress. Survival rates of the rice genotypes, their initial plant height, and shoot elongation at 9-day and 14-day submergence stress showed that seedling elongation (escape strategy) or reduction of elongation compared to control plants (quiescence strategy) under submergence stress cannot be used as phenotypic markers for selecting rice genotypes for submergence tolerance in rice. Further, the escape strategy or the quiescence strategy was not unique to the genotype, and the survival strategy of some rice genotypes changed with prolonged submergence stress. The escape strategy tended to be an SOS (Save Our Souls) strategy under prolonged submergence stress from 9 days to 14 days. No correlations between initial plant height and survival rate or survival rate and the height gain or reduction at 9-day and 14-day submergence stress showed that the submergence tolerance mechanism in rice was genotype-specific. The submergence-tolerant and moderately tolerant rice genotypes could be further investigated in future studies.

Keywords: Improved rice varieties, seedling stage, Sri Lanka traditional rice accessions, submergence tolerance.

INTRODUCTION

According to current trajectories, the world population will become 10 billion by 2056 (Persaud *et al.,* 2018), and rice consumption will be 360 million tons in 2050 (Timmer *et al.,* 2010). In the global climate change scenario, floods have increased by 65% in the last 25 years (FOASTAT, 2022). The total rice cultivation area in the world is 164.19 million hectares, and 20 million hectares of the land are located in flood plains in Asia (Manikmas, 2008; Redfern *et al.,* 2012; Singh *et al.,* 2016). Around 90% of global rice production is from eleven countries in Asia, and 45% of the rice cultivating lands in Asia are rain-fed (Rai, 1999).

The annual economic loss in rice production by flood in the world is recorded as one billion US dollars (Manikmas, 2008) and threatens global food security. Food security has three facets: malnutrition, lack of materials, and socio-cultural deprivation (Hendriks, 2015). Disappearance of traditional accessions and knowledge has been identified as a socio-cultural impact of food insecurity (Saint Ville *et al.,* 2019). The species that evolved in diverse natural habitats acquire numerous tolerances since they have adapted to local conditions. Hence, traditional rice accessions are a treasure for buffering the rice gene pool for food security. Submergence-tolerant traditional rice accessions are still cultivated in India (Ram *et al.,* 2002) and cultivating such traditional accessions ensures a local food supply in marginal environments (Pretty & Hine, 2000). However, naturally

* Corresponding author (lankaranawake@hotmail.com; https://orcid.org/0000-0003-0517-9911)

evolved submergence-tolerant rice accessions have been replaced in the irrigated commercial rice cultivation system.

Sri Lankan traditional rice accessions have been identified as a source of many abiotic and biotic stress tolerances, and submergence tolerance has been assessed at the seedling stage (Ranawake & Hewage, 2014) and post-germination stage (Ranawake *at el.,* 2010). Further, indigenous rice genotypes have been screened for submergence tolerance in different studies (Goswami *et al.,* 2017; Kumar *et al.,* 2017).

Submergence occurs in two different conditions: partial submergence and complete submergence. Under partial submergence conditions, a part of the plant is covered by water, initiating metabolic changes inside the plant (Nishiuchi *et al.,* 2012). Under complete submergence conditions, the entire plant including the leaf tip is covered by water, and the ability of a rice plant to survive 10–14 days of complete submergence and renew its growth when the water subsides is defined as complete submergence tolerance (Catling, 1992). Generally, lowland rice species cannot tolerate submergence stress for more than two weeks (Mittal *et al.,* 2022).

There are two different survival strategies in rice under submergence stress: escape strategy and quiescence strategy. Deepwater rice varieties follow escape strategy to bring the canopy above the water level faster. Ethylene elongates shoots in rice under submergence stress (Jackson, 2008), and ethylene promotes carbohydrate metabolism and adventitious root formation (Fukao & Bailey-Serres, 2008). The ethylene production rate in completely submerged rice coleoptiles has coincided with the coleoptile elongation rate under submergence stress (Kato-Noguchi, 2001). Some rice varieties reported elongating of shoots up to 25 cm/day under submergence stress (Vergara *et al.,* 2014). Two genes, *SK1* and *SK2,* assist rice plants in elongating their internodes during submergence (Nishiuchi *et al.,* 2012). The aerenchyma develops in the leaves, stems, and roots, facilitating internal aeration from shoot to root (Winkel *et al.,* 2013). The aerenchyma consists of air-filled space and helps to survive under submergence conditions. The aerenchyma is present in plants even under well-drained conditions and improves further when the soil becomes waterlogged (Zhang *et al.,* 2015).

The wetland rice type follows the quiescence strategy that limits plant elongation under submergence stress, to survive by conserving carbohydrate reservoirs. The submergence-tolerant QTL located on chromosome number 9 in rice is named *SUB1* (Bailey-Serres *et al* 2010; dos Santos *et al.,* 2017; Kuanar *et al.,* 2019). The *SUB1* locus is responsible for submergence tolerance and for post submergence adaptability by regaining photosynthesis (Nurrahma *et al.,* 2022), and it is a polygenic locus that encodes a few ethylene-responsive factor (ERF) DNA-binding proteins (Afrin *et al.,* 2018). The *SUB1* locus has been introgressed into high-yielding varieties through marker assisted selection (Ray *et al.,* 2022). The Sri Lankan traditional rice accessions, *Goda Heenati, Kurkaruppan,* and *Thavalu,* also possess *SUB1* (Panda *et al.,* 2021).

The *SUB1* QTL contains three ERF genes; *SUB1A, SUB1B*, and *SUB1C*. *SUB1A* has two alleles, namely *SUB1A-1* and *SUB1A-2,* that differ due to a single nucleotide polymorphism (Xu *et al.,* 2006). The *ERF66* and *ERF67* genes that are targeted by *SUB1A-1* downstream are directly responsible for submergence tolerance in rice (Lin *et al.,* 2019). *SUB1* regains photosynthesis (Nurrahma *et al.,* 2022) and reduces shoot elongation under flooding (Sarkar *et al.,* 2014). Contrary to this, the rice variety *FR13A* exhibited slower shoot elongation and additional biomass accumulation to recover better than a rice variety with the *SUB1* gene under submergence stress (Singh *et al.,* 2014). *FR13A* carries both *SUB1A* and *SK* genes (Oe *et al.,* 2022) and a similar result has been reported by Samanta *et al.* (2022). In principle, this proves the coexistence of escape strategy and quiescence strategy in some of the rice genotypes. Coexistence of both mechanisms in rice cultivars have also been reported in Amazon wild rice species *O. grandiglumis,* by exhibiting quiescence strategy at the seedling stage and escape strategy at the vegetative stage (Okishio *et al.,* 2014). Hence, individual rice genotypes must be studied for submergence tolerance and its mechanism.

Screening rice cultivars by imposing submergence stress at different growth stages has been practised in many studies; post-germination (Ranawake *et al.,* 2010), seedling emergence stage (Su *et al.,* 2022), seedling stage (Hussain, 2018), vegetative stage (Yi *et al.,* 2014), and reproductive stage (Ray *et al.,* 2017). The intensity of the submergence stress has been changed by applying submergence stress for different durations; six days (Devender Reddy & Mittra, 1985), seven days and 14 days (Saika *et al.,* 2021) 9 and 12 days (Saidur Rahman, 2018), five days, ten days, and 14 days (Ranawake *et al.,* 2014), over two weeks (Das *et al.,* 2009) and 14 days and 20 days

(Sarkar & Bhattacharjee, 2011) However, these studies have focused on evaluating rice genotypes under submergence stress while providing less attention to distinguishing the underlying mechanisms of shoot growth in different rice genotypes under submergence stress.

Submergence tolerance in rice cultivars can be evaluated by using biochemical markers after imposing submergence stress. Two identified biochemical markers for submergence tolerance (Sayani *et al.,* 2017) are *Adh1* (Rahman *et al.,* 2001) and *pdc1* (Quimio *et al.,* 2000). Screening by imposing submergence stress on farmer fields (Mishra *et al.,* 1996; Das *et al.,* 2009; Sarkar *et al.,* 2009), artificial tanks (Hansen *et al.,* 1986; Das *et al.,* 2009; Goswami *et al.,* 2017), and laboratory conditions (Kumar *et al.,* 2017; Sayani *et al.,* 2017) has been reported with promising results.

In the present study, thirty improved rice varieties, including four submergence tolerant check varieties, and sixty-two traditional rice accessions were screened for complete submergence tolerance at the two-week-old seedling stage to explore submergence tolerant levels and the mode of the tolerance mechanism under submergence stress.

MATERIALS AND METHODS

The study was carried out at the Faculty of Agriculture, University of Ruhuna, Mapalana, Kamburupitiya, Sri Lanka (Latitude 6.06105° or 6° 3' 40" North, Longitude 80.56586° or 80° 33' 57" East). Twenty-six (26) improved rice varieties and sixty-two (62) traditional rice accessions, along with four submergence tolerant check varieties, *IRRISub1*, *IRRI64*, *Swarnasub1*, and *Sambamasuri,* were included in the study. Traditional rice accessions and improved rice varieties (referred to as rice genotype hereafter) were collected from Plant Genetic Resources Centre, Gannoruwa, Sri Lanka.

Method of screening traditional rice accessions and improved rice varieties for submergence tolerance at the seedling stage

Dormancy broken and surface sterilized seeds were kept in an incubator at 35 ^{o}C under dark conditions with enough water for 7 ds for germination. The experiment was carried out following a randomized complete block design (RCBD) with 4 replicates, and 10 seedlings were used for each replicate. Uniformly germinated seedlings were planted in trays filled with homogenized soil. Two-week-old seedlings were subjected to 9-day, and 14-day complete submergence stresses separately. The control experiment was maintained without submergence stress. After the complete submergence period, plants were kept for recovery under de-submerged conditions for 2 wks. Green plant height was measured in submerged and control seedlings just before the submergence stress, and after the submergence stress (Supplementary Figure 1). The survival rate was scored after a 2-week recovery period.

$$\text{Survival rate} = \frac{\text{Number of surviving plants after recovery}}{\text{Number of plants before submergence}} \times 100$$

Submergence tolerance was calculated as survival rate. Survival rates were categorized into four groups based on the IRRI standard evaluation system (Table 1).

Table 1: Standard submergence scoring criteria (IRRI 1996).

Submergence scale	Survival rate	Category
1	100% survival (check variety)	Tolerant
3	95-99% survival	Tolerant
5	75-94% survival	Moderately tolerant
7	50-74% survival	Moderately susceptible
9	0-49% survival	Highly susceptible

The effect of submergence stress on seedling elongation was measured as height reduction or height gain during the submergence stress, as shown in the equation below.

Height gain or reduction of the submerged seedlings (cm)	=	(Average seedling height after the submergence)	_	(Average seedling height before the submergence)

The height gain of the control plants was calculated by considering the same time duration of the submerged plants.

Height gain of the height control seedlings (cm)	=	(Average seedling height on the date of de-submergence of submerged seedlings)	_	(Average seedling at two weeks)

Data analysis

Eighty seedlings of four replicates were evaluated in the submergence experiment. Genotypes were categorized into submergence tolerant levels according to survival percentage: Tolerant (95% - 100%), moderately tolerant (75% - 94%), moderately susceptible (50% - 74%), and highly susceptible (0% - 49%). The height gain of the submerged seedlings and control seedlings were calculated, and Duncan's multiple range test was performed to test for significant differences among height gain values of genotypes. In addition, correlation analysis was performed to see the relationship between the evaluated parameters. Data were analyzed using SAS statistical software (SAS Institute Inc., 2000).

RESULTS AND DISCUSSION

Submergence tolerance level in tested rice genotypes at 9-day and 14-day submergence stress

Traditional rice accessions: *Heenati3707, Kaluheenati4991*, *Mawee4145*, *Ratawee365,* and *Rathuheenati4992,* three improved rice varieties, namely *At306, At354, Ld371,* and check varieties*, IRRIsub1*, *IRRI64,* and *Swarnasub1* scored 100% survival rate at the 9-day submergence stress. Another check variety, *Sambamasuri,* and improved rice varieties *Bg251, At402, Bw372, Bw400*, and *Bw453* were moderately tolerant together with some traditional accessions, namely, four *Heenati* accessions (*6402, 4935, 4618, 3936*), two *Pokkali* accessions (*3573, 3562*), *Dikwee2203, Kaluwee3876, Kaluheenati7802, Kuruwee3465, Mawee5531*, and *Murungakyan3489*. Eight (8) improved varieties and 15 traditional accessions were moderately susceptible to submergence under 9-day submergence stress with a 50 - 74 % survival rate (Table 2).

Table 2: Submergence tolerance levels of rice genotypes at 9-day complete submergence stress at the seedling stage

Type	Tolerant	Moderately tolerant	Moderately susceptible	Highly susceptible
Improved rice varieties	*At354, At306* *Ld371, IRRIsub1* *IRRI64* *Swarnasub1*	*Bg251, At402* *Bw372, Bw400* *Bw453, Sambamasuri*	*Bg250, Bg352, Bg369* *Bg359, Ld368, At401,* *Bg455, At308*	*Bg300, Bg35 Bg300, Bg350, Bg94-1,* *At307At353, At362, At353, At362, At405,* *Bw367* *Ld408, At358 Ld408, At358*
Traditional rice accessions	*Heenati3707* *Kaluheenati4991* *Mawee4145* *Mawee5384* *Ratawee3655* *Rathuheenati4992* *Mawee3704* *Mawee3618*	*Dikwee2203* *Heenati6402* *Heenati4935* *Heenati4618* *Heenati3936* *Kaluwee3876* *Kaluheenati7802* *Kuruwee3465* *Mawee5531* *Murungakayan3489* *Pokkali3573* *Pokkali3562*	*Dahanala3304* *Kalubalawee5479* *Kaluheenati5191* *Kaluheenati4621* *Kuruwee3898* *Mawee8552* *Murungakayan3809* *Murungakayan3490* *Pokkali3922* *Pokkali3567* *Ratawee4580* *Rathuwee3905* *Rathuwee3473* *Suduheenati7799* *Sudurusamba4362*	*Dikwee3741, Dikwee3504* *Kaluwee3728, Kalubalawee3976* *Kuruwee3982, Mawee3683* *Mawee8551, Polayal3661* *Pokkali3881, Ratawee3466* *Ratawee3525, Heenati3998* *Dahanala3917, Kaluheenati3471* *Kalubalawee5480, Mawee8497* *Kuruwee3552, Murungakayan6263* *Murungakayan6285, Sudurusamba2202* *Murungakayan3921, Murungakayan3492* *Murungakayan3495, Rathuheenati5486* *Rathuheenati6249, Sudurusamba3671* *Suduheenati3932*

Tolerant: Survival rate 95-100%, Moderately tolerant: Survival rate 75-94%, Moderately susceptible: Survival rate 50-74%, Highly susceptible: Survival rate 0-49%

All improved submergence tolerant rice varieties (*At354*, *At306*, *Ld371*), which showed submergence tolerance at 9-day submergence stress, became moderately susceptible at 14-day submergence stress. Three improved rice varieties (*Bg251*, *At402*, *Bw372*), moderately tolerant at 9-day submergence stress, were recorded to be moderately susceptible at 14-day submergence stress. Only *Bw400* was stable at the same level of moderate tolerance at both 9-day and 14-day submergence stress (Table 3).

Table 3: Submergence tolerance levels of rice genotypes at 14-day complete submergence stress at the seedling stage

Tolerant	Moderately tolerant	Moderately susceptible	Highly susceptible		
IRRI64	*Bw400*	*Bg251*	*Bg300*	*Ld368*	*At308*
Swarnasub1	*IRRIsub1*	*At306*	*Bg352*	*Bg250*	*At362*
		At354	*Bg369*	*Bg350*	*Bw367*
		At402	*Bg455*	*Bg359*	*Bw453*
		At405	*At353*	*Bg94-1*	*Ld408*
		Bw372	*At358*	*At307*	*Sambamasuri*
		Ld371	*At401*		
Mawee3704	*Heenati4935*	*Kaluheenati4991*	*Kaluwee3876*	*Kalubalawee3976*	*Rathuheenati6249*
Mawee3618	*Mawee8552*	*Kaluheenati4621*	*Mawee5531*	*Kalubalawee5480*	*Rathueenati5486*
	Mawee4145	*Ratawee3655*	*Mawee3683*	*Kaluheenati7802*	*Rathuheenati4992*
	Ratawee3466		*Murungakayan6285*	*Kaluheenati5191*	*Suduheenati7799*
			Murungakayan6263	*Kaluhheenati3471*	*Suduheenati3932*
			Sudurusamba4362	*Kuruwee3982*	*Sudurusamba3671*
			Dahanala3917	*Kuruwee3898*	*Sudurusamba2202*
			Dahanala3304	*Kuruwee3552*	*Pokkali3922*
			Dikwee3741	*Kuruwee3465*	*Pokkali3881*
			Dikwee3504	*Mawee8497*	*Pokkali3573*
			Dikwee2203	*Mawee8551*	*Pokkali3567*
			Heenati6402	*Mawee5384*	*Pokkali3562*
			Heenati4618	*Murungakayan3921*	*Polayal3661*
			Heenati3998	*Murungakayan3809*	*Ratawee4580*
			Heenati3936	*Murungakayan3495*	*Ratawee3525*
			Heenati3707	*Murungakayan3492*	*Rathuwee3905*
			Kaluwee3728	*Murungakayan3490*	*Rathuwee3473*
			Kalubalawee5479	*Murungakayan3489*	

Tolerant: Survival rate 95-100%, Moderately tolerant: Survival rate 75-94%, Moderately susceptible: Survival rate 50-74%, Highly susceptible: Survival rate 0-49%

Rice genotypes in different submergence tolerant groups varied from 9-day to 14-day submergence stress. Out of six submergence tolerant improved rice varieties at 9-day submergence stress, only two were submergence tolerant at 14 days. Further, out of eight submergence tolerant traditional rice accessions at 9-day submergence stress, two were submergence tolerant at 14 days (Tables 2 and 3). Nineteen improved rice varieties and 53 traditional rice accessions were highly susceptible at 14-day submergence stress.

Only *Mawee4145* scored a 100% survival rate at both 9-day and 14-day stress conditions, and one-third of the traditional rice accessions that scored more than a 60% survival rate at the 9-day submergence stress (Table 4) achieved more than a 60% survival rate at the 14-day submergence stress (Table 5). The results prove that traditional rice accessions harbour more submergence-tolerant traits than the improved varieties do. *Kaluheenati4991* and *Ratawee3655,* which scored a 100% survival rate at 9-day submergence stress, had the survival rate reduced to 60% and 70%, respectively, at 14-day submergence stress.

Table 4: The survival rate, shoot elongation, and initial plant height of the best performing rice genotypes at 9-day submergence stress.

Name	SR (%)	G	IPH (cm)	Name	SR (%)	G (cm)	IPH (cm)
Traditional							
Heenati3707	100	1.3	27.4	*Rathuwee4580*	67	1.7	25.1
Kaluheenati4991	100	NE	29	*Sudurusamba4362*	67	3.6	20.5
Mawee4145	100	7.9	23.1	*Kuruwee3898*	62	6.1	12.5
Mawee5384	100	13	28.7	*Kalubalawee5479*	60	5.0	26.4
Ratawee3655	100	3.8	33.5	*Murungakayan3809*	50	5.3	21.1
Rathuheenati4992	100	10.8	25.9	*Murungakayan3490*	50	0.7	34.8
Kaluwee3876	95	NE	28.6	*Pokkali3922*	50	5.5	30.1
Kuruwee3465	89	10	13.2	*Pokkali3567*	50	3.3	25.7
Murungakayan3489	89	6.0	24.7	*Rathuwee3473*	50	4.4	24.8
Pokkali3562	89	NE	40.0	*Suduheenati7799*	50	13.4	30.0
Heenati3936	87	NE	28.3	Improved			
Heenati6402	8	NE	23.9	*At306*	100	2.0	21.3
Heenati4618	83	NE	28.5	*At354*	100	0.5	16.4
Kaluheenati7802	83	7.3	27.0	*Ld371*	100	6.3	12.1
Dikwee2203	80	1.6	29.5	*IRRIsub1*	100	6.5	17.0
Heenati4935	80	NE	31.3	*IRRI64*	100	0.2	21.0
Mawee5531	80	NE	27.5	*Swarnasub1*	100	1.6	11.1
Pokkali3573	80	8.7	20.6	*Bw400*	90	NE	19.5
Kaluheenati4621	71	1.1	23.3	*Sambamasuri*	90	4.0	11.6
Mawee8552	70	2.9	32.1	*Bw372*	80	4.4	14.7
Dahanala3304	67	8.9	21.6	*At402*	77	5.6	12.8
Kaluheenati5191	67	NE	27.4	*Bg251*	75	5.0	15.9
Ratawee3466	67	3.9	21.2	*Bw453*	75	7.3	16.8

SR:Survival rate, G: Height gain during the submergence stress, NE: Not elongated IPH: Initial plant height before submergence

Two *Mawee* accessions (*3704, 4145*) that scored 100% survival rate were better than the tolerant check variety, *IRRISub1* (90%), at 14-day submergence stress. *Ratawee3466*, *Mawee8552*, *Heenati4935*, and *Mawee3618* scored survival rates of 87%, 86%, 75%, and 75%, respectively, at 14-day submergence stress (Table 5). The Sri Lankan traditional rice gene pool is comparatively rich in submergence tolerant traits. Compared to that, none of the rice lines scored a 100% survival rate out of 525 lines in screening for submergence tolerance (Nishanth *et al.,* 2017) and three lines out of fourteen reported a 99% survival rate at 24-day submergence stress at the seedling stage (Sultana *et al.,* 2019).

Submergence tolerance mechanism in tested rice genotypes at 9-day and 14-day submergence stress

Among traditional accessions that scored a 100% survival rate at 9-day submergence stress, only *Kaluheenati4991* showed reduced height compared to the control plants. Other than *Kaluheenati*, all traditional rice accessions that showed 100% survival were elongated compared to the control plants at 9-day submergence stress (Table 4). All the improved rice varieties that scored more than 75% survival rate at 9-day submergence stress elongated under the stressed conditions compared to the control plants, other than *Bw400,* which achieved a 90% survival rate. Interestingly, among improved rice varieties, only the *Bw400* variety remained in the same moderately tolerant (survival rate 75% - 90%) group at both 9-day and 14-day submergence stress (Table 5 and 6).

Table 5: Survival rate, shoot elongation, and initial plant height of the best-performed rice genotypes at 14-day submergence stress.

Name	SR (%)	G (cm)	IPH (cm)
Traditional rice			
Mawee4145	100	NE	32.9
Mawee3704	100	NE	37.3
Ratawee3466	87	2.3	27.2
Mawee8552	88	0.7	34.4
Heenati4935	75	NE	32.3
Mawee3618	75	NE	33.4
Kaluheenati4621	71	4.7	23.5
Ratawee3655	70	NE	37.4
Kaluheenati4991	60	4.3	23.4
Improved rice			
IRRI64	100	NE	22.7
Swarnasub1	100	1.8	12.5
IRRIsub1	90	NE	17.9
Bw400	83	8.0	17.5
At405	71	NE	13.5
Ld371	67	NE	16.3
At306	62	NE	22.6
Bg251	50	3.8	15.3
At354	50	0.6	14.5
At402	50	NE	17.4
Bw372	50	5.0	14.2

SR:Survival rate, G: Height gain during the submergence stress, NE: Not elongated IPH: Initial plant height before submergence

Kaluheenati4991, *Kaluwee3876*, *Pokkali3562*, *Heenati* (*3936, 6402, 4618, 4935*), and *Mawee5531* traditional accessions that showed reduced plant height compared to the control plants at 9-day submergence stress scored more than an 80% survival rate. Among them, only *Kaluheenati4991* scored more than a 60% survival rate at the 14-day submergence stress. *Kaluheenati4991* did not elongate at 9-day submergence, but it elongated at 14-day submergence stress. The only improved rice variety that did not elongate at 9-day submergence stress, *Bw400*, was also elongated at 14-day submergence stress. *Mawee4145* behaved the other way; it elongated at 9-day submergence stress and did not elongate at 14-day submergence stress. The elongation of rice genotypes at 9-day (Table 5) and 14-day (Table 6) submergence stress varied regardless of tolerance level (Table 7).

The improved and traditional rice genotypes were prepared according to the descending order of height gain at 9-day and 14-day submergence stress. Twenty-five of each rice genotype that followed the escape strategy at 9-day (Table 5) and 14-day (Table 6) submergence stress and the quiescence strategy at 9-day and 14-day (Table 7) submergence stress were selected to show the submergence tolerance levels.

In the highest height gain group, rice genotypes that followed the escape strategy at 9-day submergence stress, were in all tolerant (20%), moderately tolerant (28%), moderately susceptible (8%), and highly susceptible (44%) categories (Table 6). However, by 14-day submergence stress, 92% of rice genotypes with the highest height gain were highly susceptible (Table 6). This emphasizes that elongation under submergence stress is a successful strategy for a relatively short (9 days) submergence period to escape the stress. Elongation under prolonged submergence stress (14 days) is the last option or SOS mechanism for the rice seedlings to escape submergence stress. All the genotypes selected for this pathway would not survive in the end. Hence, elongation is not a phenotypic marker for submergence tolerance or susceptibility, at least for the studied materials at 9-day or 14-day submergence stress. A negative correlation between shoot elongation and the survival rate under submergence at the seedling stage has been reported (Setter & Laureles, 1996). But deep water rice stimulates shoot elongation during submergence to reach photosynthetic parts to the water surface. This escape reaction is controlled by an ethylene synthesis (Fukao & Bailey-Serres, 2008). The survival mechanism of deep-water rice genotypes is to elongate under submergence stress, sometimes up to 25 cm/day (Vergara *et al.,* 2014). The submergence susceptibility under submergence stress in shoot elongation is due to excessive consumption of carbohydrates which leads to plant death (Mackill *et al.,* 2012). This is why a strong negative correlation is observed between survival percentage and plant elongation under submergence stress (Panda & Sarkar, 2013).

Table 6: Tolerance levels of twenty-five rice genotypes that followed escape strategy during 9-day and 14-day submergence stress

9-day					14-day				
Name	THG (cm)	CHG (cm)	THG-CHG (cm)	Survival rate (%)	Name	THG (cm)	CHG (cm)	THG-CHG (cm)	Survival rate (%)
Traditional									
Suduheenati7799	13.4 ^{a}	0.6 ^{jk}	12	Moderately susceptible	*Pokkali3922*	16.9 ^{a}	2.1 ^{ijk}	14.8	Highly susceptible
Mawee5384	13. ^{ab}	0.8 ^{jk}	12.2	Tolerant	*Suduheenati3932*	16.1 ^{ab}	5.8 ^{f}	10.3	Highly susceptible
Dikwee3504	12.7 ^{ab}	3.0 ^{cdefg}	9.7	Highly susceptible	*Kaluheenati3471*	15.5 ^{b}	3.5 ^{gh}	12.0	Highly susceptible
Murungakayan3495	11.9 ^{b}	4.6 ^{b}	7.3	Highly susceptible	*Murungakayan3489*	11.7 ^{c}	2.7 ^{hij}	9.0	Highly susceptible
Kuruwee3982	11.8 ^{b}	3.3 ^{bcdef}	8.5	Highly susceptible	*Pokkali3562*	10.7 ^{d}	4.3 ^{g}	6.3	Highly susceptible
Mawee3704	10.5 ^{c}	2.8 ^{defgh}	7.7	Highly susceptible	*Kaluwee3876*	9.3 ^{e}	0.8 ^{k}	8.5	Highly susceptible
Rathuheenati4992	10.2 ^{cd}	7.8 ^{a}	2.3	Tolerant	*Sudurusamba2202*	8.1 ^{fg}	10.7 ^{bc}	-2.6	Highly susceptible
Kuruwee3465	10 ^{cde}	1.4 ^{hijk}	8.6	Moderately tolerant	*Heenati4618*	7.3 ^{fghi}	3.2 ^{ghi}	4.1	Highly susceptible
Mawee3618	9.2 ^{defg}	0.8 ^{jk}	8.4	Highly susceptible	*Murungakayan6285*	7.1 ^{ghij}	10.7 ^{bc}	-3.6	Highly susceptible
Dahanala3304	8.9 ^{defg}	2.5 ^{efgh}	6.4	Moderately susceptible	*Dikwee3741*	7.0 ^{hljk}	3.8 ^{gh}	3.2	Highly susceptible
Pokkali3573	8.7 ^{efghi}	0.4 ^{k}	8.3	Moderately tolerant	*Mawee5384*	6.5 ^{ijkl}	0.7 ^{k}	5.8	Highly susceptible
Murungakayan3492	8.1 ^{fghij}	4.3 ^{bc}	3.8	Highly susceptible	*Pokkali3573*	6.2 ^{jklmn}	1.2 ^{k}	5.0	Highly susceptible
Mawee4145	7.9 ^{ghijk}	7. 8 ^{bcde}	0.1	Tolerant	*Polayal3661*	6.0 ^{klmno}	13.1 ^{a}	-7.6	Highly susceptible
Rathuheenati5486	7.6 ^{hijkl}	2.2 ^{fgi}	5.2	Highly susceptible	*Kuruwee3898*	5.9 ^{klmno}	12.9 ^{a}	-6.9	Highly susceptible
Pokkali3881	7.5 ^{hijkl}	6.9 ^{a}	0.6	Highly susceptible	*Mawee8497*	5.7 ^{lmno}	1.8 ^{jk}	3.9	Highly susceptible
Kaluheenati7802	7.3 ^{ijklm}	1.4 ^{ijk}	5.9	Moderately tolerant	*Murungakayan6263*	5.0 ^{0}	0.8 ^{k}	4.2	Highly susceptible
Dahanala3917	7.0 ^{jklm}	1.7 ^{ghijk}	5.3	Highly susceptible	Improved				
Kuruwee3898	6.1 ^{m}	6.6 ^{a}	-0.5	Moderately susceptible	*Bg94-1*	8.3 ^{f}	10.7 ^{bc}	-2.44	
Murungakayan3489	6.0 ^{m}	2.8 ^{defgh}	3.2	Moderately tolerant	*Bw400*	8.0 ^{fgh}	4.0 ^{gh}	3.98	Highly susceptible
Bg94-1	9.5 ^{cdef}	6.6 ^{a}	2.9	Highly susceptible	*Bg350*	6.8 ^{ijkl}	7.0 ^{e}	-0.27	Highly susceptible
Bw453	7.2 ^{jklm}	2.0 ^{fghij}	5.3	Moderately tolerant	*At353*	6.4 ^{jklm}	1.5 ^{jk}	4.81	Highly susceptible
Bg350	6.5 ^{klm}	1.7 ^{hijk}	4.9	Highly susceptible	*Bg455*	5.9 ^{lmno}	8.7 ^{d}	-2.83	Highly susceptible
IRRIsub1	6.5 ^{klm}	0.6 ^{jk}	5.9	Tolerant	*Bg250*	5. 8 ^{lmno}	11.0 ^{b}	-5.27	Highly susceptible
Ld371	6.3 ^{m}	4.0 ^{bcd}	2.2	Tolerant	*Bg352*	5.3 ^{mno}	11.2 ^{b}	-5.88	Highly susceptible
Bg251	5.9 ^{m}	7.0 ^{a}	-0.8	Moderately tolerant	*Ld408*	5.2 ^{no}	4.1 ^{g}	1.11	Highly susceptible
					Bw372	5.0 ^{m}	9.6 ^{cd}	-4.57	Highly susceptible

The means of the same letters are not significantly different. THG: Height gain under submergence stress, CHG: Height gain in control plants, Tolerant: Survival rate 95-100%, Moderately tolerant: Survival rate 75-94%, Moderately susceptible: Survival rate 50-74%, Highly susceptible: Survival rate 0-49%

Setter *et al*. (1997) concluded that elongation and survival under submergence stress rarely overlap. Contrary to this theory, Chen *et al.,* (2010) have reported that plant elongation and carbohydrate levels are not significantly correlated in plants undergoing submergence stress. Supporting this, Barik *et al.,* (2020) said that the five most submergence-tolerant rice genotypes performed better than the standard positive control of *FR 13A* and significantly elongated under submergence stress.

Table 7: Tolerant levels of rice genotypes followed the quiescence strategy under 9-day and 14-day complete submergence stress

	9-day			14-day	
Name	CHG (cm)	Tolerant level	Name	CHG (cm)	Tolerant level
Heenati4935	3.3 [de]	Moderately tolerant	*Rathuheenati6249*	1.0 [mn]	Highly susceptible
Polayal3661	6.0 [b]	Highly susceptible	*Murungakayan3492*	0.6 [n]	Highly susceptible
Mawee3683	3.8 [cd]	Highly susceptible	*Mawee4145*	5.8 [fg]	Tolerant
Heenati3936	3.2 [de]	Moderately tolerant	*Murungakayan3490*	8.6 [cd]	Highly susceptible
Kalubalawee3976	5.5 [b]	Highly susceptible	*Sudurusamba3671*	7.5 [de]	Highly susceptible
Ratawee3466	2.7 [de]	Highly susceptible	*Mawee3618*	1.4 [lmn]	Moderately tolerant
Kaluheenati3471	5.0 [b]	Highly susceptible	*Rathuheenati5486*	4.1 [nij]	Highly susceptible
Pokkali3562	2.5 [def]	Moderately tolerant	*Kaluheenati7802*	1.2 [lmn]	Highly susceptible
Kaluwee3876	0.7 [h]	Moderately tolerant	*Pokkali3881*	16.5 [a]	Highly susceptible
Sudurusamba3671	4.9 [bc]	Highly susceptible	*Mawee3704*	3.7 [ijk]	Tolerant
Heenati6402	3.1 [de]	Moderately tolerant	*Rathuwee3905*	2.4 [klm]	Highly susceptible
Kaluheenati4991	1.0 [h]	Tolerant	*Heenati4935*	3.3 [ijk]	Moderately tolerant
Heenati4618	1.4 [fgh]	Moderately tolerant	*Rathuheenati4992*	9.7 [bc]	Highly susceptible
Mawee5531	3.2 [de]	Moderately tolerant	*Rathuwee3473*	3.5 [ijk]	Highly susceptible
Kaluheenati5191	8.9 [a]	Moderately susceptible	*Ratawee4580*	0.8 [mn]	Highly susceptible
Murungakayan3490	8.6 [a]	Moderately susceptible	*Murungakayan3921*	4.8 [ghi]	Highly susceptible
Heenati3998	3.0 [de]	Highly susceptible	*Heenati3998*	1.1 [lmn]	Highly susceptible
Kaluheenati4621	2.4 [efg]	Moderately susceptible	*Ld368*	3.5 [ijk]	Highly susceptible
Bg250	4.9 [bc]	Moderately susceptible	*At405*	6.4 [ef]	Moderately susceptible
Bg369	1.4 [fgh]	Moderately susceptible	*At362*	3.1 [jk]	Highly susceptible
At353	1.1 [h]	Highly susceptible	*At401*	2.7 [klmn]	Highly susceptible
At354	1.2 [gh]	Tolerant	*Ld371*	2.7 [jkl]	Moderately susceptible
Bw400	3.2 [de]	Moderately tolerant	*At306*	10.7 [b]	Moderately susceptible
			At402	2.7 [jkl]	Moderately susceptible
			IRRI64	5.7 [fgh]	Tolerant

The means of the same letters are not significantly different. CHG: Height gain of the control plants, susceptible: Tolerant: Survival rate 95-100%, Moderately tolerant: Survival rate 75-94%, Moderately susceptible: Survival rate 50-74%, Highly susceptible: Survival rate 0-49%

In the genotypes, there was no height gain during the submergence stress; rice genotypes that followed the quiescence strategy belonged to all tolerant (12%), moderately tolerant (32%), moderately susceptible (24%), and highly susceptible (32%) categories at the 9-day submergence stress. Altogether, 44% of rice genotypes that followed the quiescence strategy were moderately tolerant or tolerant.

The highly susceptible rice genotypes that followed the quiescence strategy (18.9%) were less than that of rice genotypes that followed the escape strategy (81.08%) at 9-day submergence stress. Similarly, 23.61% followed the quiescence strategy, and 76.38% followed the escape strategy at 14-day submergence stress. These findings emphasize that the quiescence strategy is much more stable than the escape strategy for survival under submergence stress when the submergence condition continues (increased from 18.9% to 23.61%). The quiescence strategy is said to be led by the *SUB1* gene in rice that limits ethylene production for reduce shoot elongation under submergence stress (Sarkar *et al.,* 2014). In a previous study where fourteen rice lines were tested for submergence tolerance, only three lines scored a 99% survival rate under 24-day submergence stress at the seedling stage. They had shown lower elongation rates (Sultana *et al.,* 2019) that derives from *SUB1A*. The Sri Lankan submergence-tolerant traditional rice accession *Godaheenati* and another accession *Vaidehi* have been reported to practise another submergence-tolerant mechanism unrelated to *SUB1* (Jackson & Ram, 2003).

However, *Godaheenati* possesses *SUB1* (Panda *et al.,* 2021). *SUB1* carrying genotypes that exclude the quiescence strategy reveals that *SUB1* alone does not decide the quiescence strategy in rice, or other gene expressions override the *SUB1* activity. The present study's findings propose that limited growth under submergence stress alone is insufficient to develop submergence tolerance in rice seedlings.

Pearson's correlation coefficients were calculated to find possible correlations among initial plant height, survival rate, height gain or reduction under submergence stress at 9-day and 14-day submergence stress. There was no significant correlation between any of the two parameters at 9-day or 14-day submergence stress other than a weak correlation between initial plant height and survival rate in traditional rice accessions at 14-day submergence stress (Table 8). This finding emphasizes that the submergence tolerance mechanism is genotype specific. Further, the correlation analysis reveals that submergence tolerance is not directly governed by elongation or reduction of plant height during submergence stress. Quiescence strategy or escape strategy alone is not capable of tolerating submergence stress. At the same time, correlation analysis indicates that the initial plant height is not a factor in deciding rice seedlings' submergence tolerance level. Submergence tolerance is a complex mechanism that many factors involved in different scales other than quiescence or escape strategy. Submergence tolerance has been identified as a complex mechanism involving balancing carbohydrate utilization for shoot elongation and maintenance and gibberellic acid function that restricts shoot elongation (Setter *et al.,* 1997). Hence, there would not be distinct groups of genotypes in rice that undergo quiescence or escape strategy at all submergence stress conditions at all growth stages.

Table 8: The correlation coefficient of initial plant height, survival rate, height gain and survival rate at 9-day and 14-day complete submergence stress

		9-day		14-day	
Genotype	Correlation	r	α	r	α
Improved varieties	Initial plant height × survival rate	0.127	0.505	0.145	0.445
	Height gain × survival rate	0.133	0.488	0.301	0.106
Traditional accessions	Initial plant height × survival rate	0.142	0.271	0.328**	0.009
	Height gain × survival rate	-0.060	0.644	-0.183	0.156
Improved tolerant	Initial plant height × survival rate	0.173	0.590	0.003	0.997
	Height gain × survival rate	-0.515	0.015	-0.729	0.271
Traditional tolerant	Initial plant height × survival rate	0.061	0.811	0.293	9.573
	Height gain × survival rate	0.370	0.136	-0.271	0.604
Improved moderately susceptible	Initial plant height × survival rate Height gain × survival rate	-0186 0.577	0.659 0.134	0.123 -0.713	0.794 0.072
Traditional moderately susceptible	Initial plant height × survival rate	-0.305	0.269	0.401	0.737
	Height gain × survival rate	-0.333	0.226	-0.334	0.783
Traditional highly susceptible	Initial plant height × survival rate	0.119	0.538	0.071	0.615
	Height gain × survival rate	-0.600	0.756	0.071	0.611
Improved highly susceptible	Initial plant height × survival rate	0.386	0.274	0.071	9.772
	Height gain × survival rate	0.589	0.373	-0.169	0.488

r: Pearson's correlations, α: significant level, Tolerant: Survival rate 75-100%, Moderately susceptible: Survival rate 50-74%, Highly susceptible: Survival rate 0-49%

CONCLUSION

Mawee accessions *3704* and *3618* were submergence tolerant, and *Ratawee3466*, *Mawee (8552, 4145)* and *Heenati4935* were moderately submergence tolerant. The improved *Bw400* rice variety can be recommended as a moderately tolerant rice variety according to the IRRI-adapted screening technique. Submergence-tolerant rice genotypes in the present study must be evaluated at other growth stages. Promising rice genotypes can be incorporated into future breeding programs to develop submergence-tolerant rice varieties.

The submergence tolerance mechanism in rice is genotype-specific. Further, the same rice genotype adapted different strategies to survive under different periods of submergence stress. Hence, the same submergence-tolerant approach cannot be expected at any submergence stress at any growth stage.

The quiescence strategy is much more stable for prolonged submergence stress. The escape strategy is very common as an SOS strategy under prolonged submergence stress.

Initial plant height, shoot elongation, or reduction of shoot height gain under submergence stress compared to control plants may not be phenotypic markers for selecting rice genotypes for submergence tolerance. However, the survival rate of the rice seedlings after the recovery period followed by the submergence stress is a successful direct method to evaluate the submergence tolerance in rice genotypes. Future studies must examine reliable submergence-tolerant physiological markers for screening rice genotypes.

Acknowledgement

The authors would like to acknowledge the financial support of NRC (12-027), Indo-Sri Lanka PoC, and ICGEB/CRP/SRI/13-01 for financial assistance, and the Plant Genetic Resources Centre (PGRC), Gannoruwa, Sri Lanka, for providing traditional rice accessions.

REFERENCES

Afrin W., Nafis M.H., Hossain Muhammed Ali., Islam M.M. & Hossain Md Amir (2018). Responses of rice (*Oryza sativa* L.) genotypes to different levels of submergence. *Comptes Rendus - Biologies* **341**: 85–96.
DOI: https://doi.org/10.1016/j.crvi.2018.01.001

Bailey-Serres J., Fukao T., Ronald P., Ismail A., Heuer S. & Mackill D. (2010). Submergence tolerant rice: SUB1's journey from landrace to modern cultivar. *Rice* **3**: 138–147.
DOI: https://doi.org/10.1007/s12284-010-9048-5

Barik J., Kumar V., Lenka S.K. & Panda D. (2020). Assessment of variation in morpho-physiological traits and genetic diversity in relation to submergence tolerance of five indigenous lowland rice landraces. *Rice Science* **27**: 32–43.
DOI: https://doi.org/10.1016/j.rsci.2019.12.004

Catling D. (1992). Deepwater rice cultures in the Ganges-Brahmaputra Basin. In: *Rice in Deep Water,* pp. 213–244. Palgrave Macmillan, London, UK.
DOI: https://doi.org/10.1007/978-1-349-12309-4_17

Chen X., Pierik R., Peeters A.J.M., Poorter H., Visser E.J.W., Huber H., de Kroon H. & Voesenek L.A.C.J. (2010). Endogenous abscisic acid as a key switch for natural variation in flooding-induced shoot elongation. *Plant Physiology* **154**: 969–977.
DOI: https://doi.org/10.1104/pp.110.162792

Das K.K., Panda D., Sarkar R.K., Reddy J.N. & Ismail A.M. (2009). Submergence tolerance in relation to variable floodwater conditions in rice. *Environmental and Experimental. Botany* **66:** 425–434.
DOI: https://doi.org/10.1016/J.ENVEXPBOT.2009.02.015

Devender Reddy M. & Mittra B.N. (1985). Effects of complete plant submergence on vegetative growth, grain yield and some biochemical changes in rice plants. *Plant and Soil* **87**: 365–374.
DOI: https://doi.org/10.1007/BF02181904

Dos Santos, R.S., da Rosa Farias, D., Pegoraro C., Rombaldi C.V., Fukao T., Wing R.A. & de Oliveira A.C. (2017). Evolutionary analysis of the SUB1 locus across the *Oryza* genomes. *Rice* **10(4)**: 1–5.
DOI: https://doi.org/10.1186/s12284-016-0140-3

FOASTAT (2022). *Production Quantities of Rice, Paddy by Country*. Food and Agriculture Organization. United Nations, Rome, Italy.

Fukao T. & Bailey-Serres J. (2008). Ethylene-A key regulator of submergence responses in rice. *Plant Science* **175**: 43–51.
DOI: https://doi.org/10.1016/j.plantsci.2007.12.002

Goswami S., Kar R.K., Paul A. & Dey, N. (2017). Genetic potentiality of indigenous rice genotypes from Eastern India with reference to submergence tolerance and deepwater traits. *Current Plant Biology* **11-12**: 23–32
DOI: https://doi.org/10.1016/j.cpb.2017.10.002

Hansen M., Busch L., Burkhardt J., Lacy W.B. & Lacy L.R. (1986). Plant Breeding and Biotechnology. *Bioscience* **36**: 29–39.
DOI: https://doi.org/10.2307/1309795

Hendriks S. (2015). The food security continuum: a novel tool for understanding food insecurity as a range of experiences. *Food Security* **7**: 609–619.

Hussain M. (2018). Phenotypic response of rice genotypes under submergence conditions at seedling stage. *Current Investigations in Agriculture and Current Research* **5(4)**: 722–726.
DOI: https://doi.org/10.32474/ciacr.2018.05.000220

IRRI (1996). *Standard Evaluation System for Rice*. IRRI, International Rice Research Institute, Philippine.

Jackson M.B. (2008). Ethylene-promoted elongation: an adaptation to submergence stress. *Annals of Botany* **101**: 229–248. DOI: https://doi.org/10.1093/aob/mcm237

Jackson M.B. & Ram P.C. (2003). Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. *Annals of Botany* **91**: 227–241. DOI: https://doi.org/10.1093/aob/mcf242

Kato-Noguchi H. (2001). Submergence tolerance and ethanolic fermentation in rice coleoptiles. *Plant Production Science* **4**(1): 62–65. DOI: https://doi.org/10.1626/pps.4.62

Kuanar S.R., Molla K.A., Chattopadhyay K., Sarkar R.K. & Mohapatra P.K. (2019). Introgression of Sub1 (SUB1) QTL in mega rice cultivars increases ethylene production to the detriment of grain- filling under stagnant flooding. *Scientific Report* **9**(1): 18657 1–12. DOI: https://doi.org/10.1038/s41598-019-54908-2

Kumar S., Dwivedi S.K., Kumar R., Bhakta N., Prakash V., Rao K.K., Kumar R., Yadav S., Choubey A.K. & Mishra J.S. (2017). Screening of different rice germplasm against multiple disease under submergence condition in middle Indo Gangetic plain. *International Journal of Current Microbiology and Applied Sciences* **6**(5): 335–339. DOI: https://doi.org/10.20546/ijcmas.2017.605.038

Lin *et al*. (20 authors) (2019). Regulatory cascade involving transcriptional and N-end rule pathways in rice under submergence. *Proceedings of the National Academy of the Sciences USA* **116**: 3300–3309. DOI: https://doi.org/10.1073/pnas.1818507116

Mackill D.J., Ismail A.M., Singh U.S., Labios R.V. & Paris T.R. (2012). Development and rapid adoption of submergence-tolerant (Sub1) rice varieties. *Advances in Agronomy* **115**: 299–352. DOI: https://doi.org/10.1016/B978-0-12-394276-0.00006-8

Manikmas M.O. (2008). Developing submergence-tolerant rice varieties in Indonesia. *Journal of Sub1 News* **2**: 4–5.

Mishra S.B., Senadhira D. & Manigbas N.L. (1996). Genetics of submergence tolerance in rice (*Oryza sativa* L.). *Field Crop Research* **46**: 177–181. DOI: https://doi.org/10.1016/0378-4290 (95)00088-7

Mittal L., Tayyeba S. & Sinha A.K. (2022). Finding a breather for *Oryza sativa*: Understanding hormone signalling pathways involved in rice plants to submergence stress. *Plant Cell and Environment* **45(2)**: 279–295. DOI: https://doi.org/10.1111/pce.14250

Nishanth G.K., Dushyanthakumar B.M., Gangaprasad S., Gowda T.H., Nataraju S.P. & Shashidhar H.E. (2017). Screening and genetic variability studies in submergence tolerance rice germplasm lines under flood prone lowlands of hill zone of Karnataka. *International Journal of Current Microbiology and Applied Sciences* **6**: 1254–1260. DOI: ttps://doi.org/10.20546/ijcmas.2017.607.152

Nishiuchi S., Yamauchi T., Takahashi H., Kotula L. & Nakazono M. (2012). Mechanisms for coping with submergence and waterlogging in rice. *Rice* **5**: 1–4. DOI: https://doi.org /10.1186/1939-8433-5-2

Nurrahma A.H.I., Yabuta S., Junaedi A. & Sakagami J.I. (2022). Different survival strategies involve carbon translocation rather than de novo C assimilation under complete submergence in rice plant. *Photosynthesis Research* **154**(2): 183–193. DOI: https://doi.org/10.1007/s11120-022-00959-y

Oe S., Sasayama D., Luo Q., Fukayama H., Hatanaka T. & Azuma T. (2022). Growth responses of seedlings under complete submergence in rice cultivars carrying both the submergence-tolerance gene SUB1A-1 and the floating genes SNORKELs. *Plant Production Science* **25**: 70–77. DOI: https://doi.org/10.1080/1343943X.2021.1943465

Okishio T., Sasayama D., Hirano T., Akimoto M., Itoh K. & Azuma T. (2014). Growth promotion and inhibition of the Amazonian wild rice species *Oryza* grandiglumis to survive flooding. *Planta* **240**(3): 459–469. DOI: https://doi.org/10.1007/s00425-014-2100-8

Panda D., Barik J. & Sarkar R.K. (2021). Recent advances of genetic resources, genes and genetic approaches for flooding tolerance in rice. *Current Genomics* **22**: 41–58. DOI: https://doi.org/10.2174/1389202922666210114104140

Panda D. & Sarkar R.K. (2013). Structural carbohydrates and lignifications associated with submergence tolerance in rice (*Oryza sativa* L.). *Journal of Stress Physiology and Biochemistry* **9**: 299–306.

Persaud A., Bhat P.S., Ventriglio A. & Bhugra D. (2018). Geopolitical determinants of health. *Industrial Psychiatry Journal* **27**: 308.

Pretty J. & Hine R. (2000). The promising spread of sustainable agriculture in Asia. *Natural Resources Forum* **24**(2): 107–121. DOI: https://doi.org/10.1111/j.1477-8947.2000.tb00936.x

Quimio *et al.* (11 authors) (2000). Enhancement of submergence tolerance in transgenic rice overproducing pyruvate decarboxylase. *Journal of Plant Physiology* **156**: 516–521. DOI: https://doi.org/10.1016/S0176-1617(00)80167-4

Rahman M., Grover A., Peacock W.J., Dennis E.S. & Ellis M.H. (2001). Effects of manipulation of pyruvate decarboxylase and alcohol dehydrogenase levels on the submergence tolerance of rice. *Australian Journal of Plant Physiology* **28**: 1231–1241.

Rai M. (1999). Rice germplasm evaluation and enhancement in India: issues, status, options, and future plan of action. *Proceedings of the International Symposium on Rice Germplasm Evaluation and Enhancement*. Arkansas Agricultural Experiment Station, USA, pp. 83–91.

Ram *et al.* (15 authors) (2002). Submergence tolerance in rainfed lowland rice: physiological basis and prospects for cultivar improvement through marker-aided breeding. *Field Crop Research* **76**(2-3): 131–152.
DOI: https://doi.org/10.1016/S0378-4290(02)00035-7

Ranawake A.L., Dahanayaka N. & Senadhipathy D.D. (2010). Evaluation of level of submergence tolerance in traditional rice cultivars at post germination stage. *Proceedings of the 8th Academic Sessions*. University of Ruhuna, Sri Lanka, pp 233.

Ranawake A.L., Amarasinghe U.G.S. & Senanayake S.G.J.N. (2014). Submergence tolerance of some modern rice cultivars at seedling and vegetative stages. *Journal of Crop and Weed* **10**: 240–247.

Ranawake A.L. & Hewage M.J. (2014). Correlation analysis of drought, salinity and submergence tolerance in some traditional rice cultivars of Sri Lanka. *International Journal of Scientific and Research Publications* **4**(7): 1–5.

Ray B.P., Nath U.K. & Azad A.K. (2022). Genetic analysis of submergence tolerance rice genotypes by intro-gression of sub1 QTL to Indica HYV through breeding populations (F 2) with Marker Assay. *American Journal of Pure and Applied Biosciencec* **4**(1): 10–21.

Ray A., Panda D. & Sarkar R.K. (2017). Can rice cultivar with submergence tolerant quantitative trait locus (SUB1) manage submergence stress better during reproductive stage? *Archives of Agronomy and Soil Science* **63**: 998–1008.
DOI: https://doi.org/10.1080/03650340.2016.1254773

Redfern S.K., Azzu N. & Binamira J.S. (2012). Rice in Southeast Asia: facing risks and vulnerabilities to respond to climate change. *Building Climate Resilience in the Agriculture Sector of Asia and the Pacific* **23**: 1–14.

Saidur Rahman (2018). Effect of submergence durations on yield and yield contributing characters of hybrid and inbred aman rice. *Asian-Australasian Journal of Bioscience and Biotechnology* **3**: 225–230.

Saikia D., Kalita J., Chutia J., Vemireddy L.N.R. & Tanti B. (2021). Dissecting the morpho-physiological and biochemical responses in some traditional rice cultivars under submergence stress. *Vegetos* **34 (1)**: 191–204.

Saint Ville A., Po J.Y.T., Sen A., Bui A. & Melgar-Quiñonez H. (2019). Food security and the Food Insecurity Experience Scale (FIES): ensuring progress by 2030. *Food Security* **11**: 483–491.
DOI: https://doi.org/10.1007/S12571-019-00936-9/TABLES/3

Samanta P., Chakrabarti A. & Dey N. (2022). Study on physiological responses with allelic diversity of Sub1A and SK loci in rice seedlings under complete submergence. *Plant Physiology Reports* **27** (2): 275-281.
DOI: https://doi.org/10.1007/s40502-022-00660-1

Sarkar R.K., Das K.K., Panda D., Reddy J.N., Patnaik S.S.C., Patra B.C. & Singh D.P. (2014). *Submergence Tolerance in Rice: Biophysical Constraints, Physiological Basis and Identification of Donors,* pp. 36. Central Rice Research Institute, Cuttck, India.

Sarkar R.K. & Bhattacharjee B. (2011). Rice genotypes with SUB1 QTL differ in submergence tolerance, elongation ability during submergence and re-generation growth at re-emergence. *Rice* **5**: 1–11
DOI: https://doi.org/10.1007/s12284-011-9065-z

Sarkar R.K., Panda D., Reddy J.N., Patnaik S.S.C., Mackill D.J. & Ismail A.M. (2009). Performance of submergence tolerant rice (*Oryza sativa*) genotypes carrying the Sub1 quantitative trait locus under stressed and non-stressed natural field conditions. *Indian Journal of Agricultural Science*s **79**: 876–883.

SAS Institute Inc. (2000). SAS Online Doc, version 8. Available at *https://www.sfu.ca/sasdoc/sashtml/main.htm.*

Sayani G., Kumar K.R., Anupam P. & Narottam D. (2017). Study of selected biochemical parameters related to submergence tolerance in rice (*Oryza sativa* L.) with special reference to land races and wild species. *Research Journal of Chemistry and Environment* **21**: 29–38.

Setter T.L., Ellis M., Laureles E.V., Ella E.S., Senadhira D., Mishra S.B., Sarkarung S. & Datta S. (1997). Physiology and genetics of submergence tolerance in rice. *Annals of Botany* **79**: 67–77.
DOI: https://doi.org/10.1006/anbo.1996.0304

Setter T.L. & Laureles E.V. 1996. The beneficial effect of reduced elongation growth on submergence tolerance of rice. *Journal of Experimental Botany* **47**: 1551–1559.
DOI: https://doi.org/10.1093/jxb/47.10.1551

Singh R. *et al*., (11 authors) (2016). From QTL to variety-harnessing the benefits of QTLs for drought, flood and salt tolerance in mega rice varieties of India through a multi-institutional network. *Plant Sciences*. **242**: 278–287.

Singh S., Mackill D.J. & Ismail A.M. (2014). Physiological basis of tolerance to complete submergence in rice involves genetic factors in addition to the SUB1 gene. *AOB Plants Journal for plant Science* **6**: 1–20.
DOI: https://doi.org/10.1093/aobpla/plu060

Su X., Wu H., Xiang J., Zhan J., Wang J., Li X., Wei Y., Dai H. & Chen H. (2022). Evaluation of submergence tolerance of different rice genotypes at seedling emergence stage under water direct seeding. *Open Access Library Journal* **09**: 1–15.
DOI: https://doi.org/10.4236/oalib.1108706

Sultana A., Islam M.M., Sultana A. & Khanom M.S.R. (2019). Screening of rice genotypes for submergence stress at seedling stage. *Journal of Agroforestry and Environment* **13**: 1–4.

Timmer C.P., Block S. & Dawe D. (2010). Long-run dynamics of rice consumption, 1960–2050. In: *Rice in the Global Economy: Strategic Research and Policy Issues for Food Security. Resources for the Future* (eds. S. Pandey, D. Byerlee & D. Dawe), pp.139–173. Los Banos, Philippines.

Vergara G.V., Nugraha Y., Esguerra M.Q., Mackill D.J. & Ismail A.M. (2014). Variation in tolerance of rice to long-term stagnant flooding that submerges most of the shoot will aid in breeding tolerant cultivars. *AOB Plants Journal for Plant Sciences* **6**: 1–16.
DOI: https://doi.org/10.1093/aobpla/plu055

Winkel A., Colmer T.D., Ismail A.M. & Pedersen O. (2013). Internal aeration of paddy field rice (*Oryza sativa*) during complete submergence - importance of light and floodwater O_2. *New Phytologist* **197**: 1193–1203.
DOI: https://doi.org/10.1111/nph.12048

Xu K., Xu X., Fukao T., Canlas P., Maghirang-Rodriguez R., Heuer S., Ismail A.M., Bailey-Serres J., Ronald P.C. & Mackill D.J. (2006). Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. *Nature* **442**: 705–708.
DOI: https://doi.org/10.1038/nature04920

Yi Y., Ella E., Ismail A.M., Woo S. & Lee C. (2014). Screening analysis for submergence tolerance of 6 rice cultivars at vegetative stages. *Proceedings of the 240th Annual Meeting of the Crop Science Society of Japan.* Crop Science Society of Japan, Japan, pp 82.

Zhang Y., Wang Z., Li L., Zhou Q., Xiao Y. & Wei X. (2015). Short-term complete submergence of rice at the tillering stage increases yield. *PLOS One* **10**(5): e0127982.
DOI: https://doi.org/10.1371/journal.pone.0127982