Experimental Agriculture (2026), vol. 62, e21, 1–14
doi:10.1017/S0014479726100428

CAMBRIDGE UNIVERSITY PRESS

RESEARCH ARTICLE

Repeated submergence stress impairs yield despite improved survival in rice

Nurudeen Alabi Salaudeen[1,2,3], Moninuola Adefolake Ayo-Vaughan[2], Emmanuel Ohiosinmuan Idehen[2] and Vimal Kumar Semwal[3]

[1]International Institute of Tropical Agriculture, Nigeria, [2]Federal University of Agriculture Abeokuta, Nigeria and [3]AfricaRice: Africa Rice Center, C/O IITA, Ibadan, Nigeria
Corresponding author: Vimal Kumar Semwal; Email: v.semwal@cgiar.org

(Received 16 June 2025 UTC; revised 21 September 2026 UTC; accepted 22 September 2026 UTC)

Abstract
Submergence stress is a major constraint to rice production in flood-prone areas. Acclimation responses are well-documented for many abiotic stresses in rice; however, the ability of rice to acclimate to repeated submergence stress periods remains unexplored. In this study, we evaluated 15 rice varieties under both single- and double-submergence stress conditions to determine whether prior exposure enhances submergence tolerance. Repeated submergence significantly reduced grain yield (GY) across most genotypes, despite improved or sustained survival in submergence-tolerant varieties. Correlation and multivariate analyses revealed that GY was strongly associated with survival, tiller number, and panicle number, whereas shoot elongation contributed little to yield variation. Although some genotypes exhibited enhanced survival following repeated submergence, this advantage did not translate into improved yield, indicating that acclimation responses are limited to survival and did not extend to productivity. These findings highlight the need for breeding strategies that integrate survival with post-submergence recovery and yield stability under recurrent flooding conditions.

Keywords: acclimation; flood tolerance; stress tolerance and rice; submergence

Introduction

Rice is a staple food in many countries of Africa and constitutes a major part of the diet for more than half of the world's population; hence, it is considered a strategic commodity crop in the world (Fukagawa and Zhiska, 2019). Consumption of rice in Africa has increased compared to other traditional cereals of Africa, such as sorghum, millet, and other root and tuber crops like cassava and yam (Seck *et al.*, 2012). Yet, the majority of sub-Saharan African countries are not self-sufficient in rice production, putting a burden on economies due to large imports of rice in the continent (Yuan *et al.*, 2024). It is necessary to increase rice production in Africa to meet the demand in rice consumption.

Flooding is a natural disaster that has a detrimental effect on plant growth and farmers' livelihoods. The effect of flash floods on plant survival seriously depends on the duration of submergence stress. This submergence stress is a condition where the entire plant is fully immersed in water (complete submergence) or at least part of the shoot terminal is maintained above the water surface (partial submergence) (Tamang *et al.*, 2015). Rice is often the only cereal that can be grown in flood-prone ecosystems (Sarkar *et al.*, 2011), but flash floods and excessive rainfall regularly affect rain-fed lowland rice in many parts of the world where floodwater remains

© The Author(s), 2026. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

for fourteen days or more (Aryalekshmi *et al.*, 2021). In recent years in many sub-Saharan African countries, rice crops have faced serious flood problems leading to large agricultural losses (Reed *et al.*, 2022; Balgah *et al.*, 2023). There have been increasing incidents of repeated cycles of complete submergence of rice crops in many parts of Africa during the main cropping wet season (WS) (July to October). Also, there have been incidents where submergence periods have exceeded a month and beyond, where no rice variety could survive. In flood-prone ecology, rice farmers generally grow traditional rice varieties that can tolerate flooding, but these usually have poor yields (Dar *et al.*, 2017). In recent years, a gene for submergence tolerance (*Sub1*) has been identified and introgressed into high-yielding rice varieties that can tolerate submergence for up to two weeks (Septiningsih *et al.*, 2009).

The *Sub1* gene is an important QTL on chromosome 9 derived from the landrace FR13A and comprises three ethylene response factor (ERF) transcription factors. The tolerant *Sub1A* allele limits shoot elongation in the form of a quiescence strategy, thereby preserving carbohydrates and improving survival during complete submergence (Xu *et al.*, 2006). In recent years, through marker-assisted backcrossing, *Sub1* has been introgressed into high-yielding rice varieties that maintain grain yield (GY) as well as survive submergence for up to two weeks (Septiningsih *et al.*, 2009). Beyond survival, *Sub1* introgressed varieties have delivered measurable on-farm benefits in flood-prone areas, reducing the yield losses and stabilizing production. However, when there is recurrent incidence of submergence within the same growing season, accumulated stress-induced constraints could cause reduction in yield even in *Sub1* introgressed lines.

When plants are exposed to environmental changes, they initiate a series of physiological, biochemical, and molecular adaptations to survive under stress conditions. These responses are crucial for rice under low-oxygen environments like submerged conditions (Kuroha *et al.*, 2020; Oladosu *et al.*, 2020). To adapt, plants upregulate antioxidative defense mechanisms, produce molecules such as ERFs, and synthesize and accumulate cryoprotectant solutes (Bailey-Serres *et al.*, 2012; Kuroha *et al.*, 2020). Additionally, they undergo modifications that protect and stabilize cellular membranes. These collective changes enable plants to adapt, survive, and maintain cellular function under adverse environmental conditions (Kuroha *et al.*, 2020). Abiotic stress acclimatory responses and benefits are well known and documented for many abiotic stresses in rice and other crops (Gupta *et al.*, 2023). However, to the best of our knowledge, there is no research reported in literature on the acclimation capacity of rice to submergence or the response of rice crops to repeated cycles of flood stress. Considering recent climatic events of repeated floods during rice cropping, there is an urgent need to identify rice varieties capable of withstanding submergence stress for more than two weeks and to identify varieties that can perform well in repeated cycles of submergence and recovery. In the present study, we evaluated the response of widely cultivated submergence-tolerant rice varieties carrying the Sub1 gene, along with non-Sub1 improved varieties and selected Nigerian landraces, to two sequential cycles of submergence stress separated by a recovery phase. The objective was to investigate the extent of stress acclimation in these genotypes by examining survival, growth, and yield-related responses under repeated submergence conditions.

Materials and methods

Experimental site and plant material

The experiments were carried out at the Africa Rice Center (Africa Rice) research station at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (Latitude 3°54′32″ E and Longitude 7°29′15″N). Screening for submergence was conducted under field conditions using specially created deep submergence tanks (depth 2 m).

Fifteen rice genotypes were obtained from the rainfed lowland breeding programme of the Africa Rice Centre based at Ibadan, Nigeria. Table 1 shows the list of varieties used in this study.

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Table 1. List of varieties and landraces used for this study.

S/N	Varieties	Remarks
1	FARO 44	Improved variety
2	FARO 52	Improved variety
3	FARO 57	Improved variety
4	FARO 60	Improved variety
5	UPIA 3	Improved variety
6	FARO 66	Improved (Sub1) variety
7	FARO 67	Improved (Sub1) variety
8	Swarna-Sub1	Improved (Sub1) variety
9	IR64-Sub1	Improved (Sub1) variety
10	Samba Masuri-Sub1	Improved (Sub1) variety
11	CHAKURAGI	Landrace
12	Ladanci	Landrace
13	TOS 6454	Landrace (Submergence tolerant)
14	R84196	Landrace
15	NERICA-L-52	Improved variety

The two experiments were conducted in the WS of 2019 and repeated in the 2020 dry season (DS). The rice genotypes were planted and evaluated for submergence tolerance in a random complete block design with three replicates in the submergence tanks. Seeds were kept in an oven for 48 h at 50°C to break the dormancy, followed by direct seeding in the submergence tanks. The experiments were designed using an alpha lattice design with 3 replicates. The plot size was 2 m × 2 rows, maintaining 22 hills per plot at a spacing of 20 cm between the hills and 30 cm between the rows. Two submergence tanks, one each for single- and double-submergence stress treatments, were used.

Submergence stress treatments

For the single-submergence stress treatment, fourteen-days-old rice seedlings were subjected to complete submergence for fourteen days by filling the submergence tank with water. . A water depth of 2 m was maintained in the submergence tank for the entire period during the stress treatment by adding water regularly. The water was drained out completely after 14 days of stress to start the recovery period. The survival rates of plants were scored twice: once immediately after the water was drained off, and the second scoring was after 21 days of the recovery period (Xu *et al*., 2000). The surviving seedlings were allowed to grow normally until their full maturity. A standing water depth of 5 cm was maintained in the tank for the remaining growth period (Xu *et al*., 2000; Septiningsih *et al*., 2009).

For the double-submergence stress treatment, fourteen-days-old rice seedlings were subjected to complete submergence for eight days, followed by recovery for 21 days in the submergence tank as described earlier. The survival rates of the rice plants were scored twice as described earlier (Septiningsih *et al*., 2009; Xu *et al*., 2000). The recovered rice seedlings were subjected to a second cycle of submergence stress for fourteen days by adding water to the submergence tank. The survival of seedlings was again scored twice: First scoring was done immediately after the water was drained off, and second scoring was after 21 days of the recovery period (Xu *et al.,* 2000). The surviving seedlings were allowed to grow normally until their full maturity. Standing water depth of 5 cm was maintained in the tank for the remaining growth period. The double-submergence treatment (8 days + 14 days) was designed to mimic natural flood recurrence patterns frequently experienced in rainfed lowland rice systems, where an early-season transient flood is often followed by a prolonged late-season submergence (Ismail *et al*., 2013). A recovery phase between the two events was included to assess whether early submergence exposure could induce physiological acclimation, a concept widely studied in drought, heat, and salinity stress, but that

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

had not previously been investigated in rice submergence tolerance. Thus, the total stress duration (8 + 14 days) does not represent continuous submergence but two discrete stress events separated by recovery, reflecting realistic field conditions rather than equalized-duration treatments. The overall single and double submergence stress treatments are also summarized in Figure S1.

Submergence treatments were imposed using regular lake water which was clean and transparent (IITA Lake, Ibadan). Although turbidity was not quantitatively measured, the water remained moderately turbid due to suspended soil particles mimicking flooding conditions commonly encountered in rainfed lowland rice systems.

Data collection

The data were collected as described by Septiningsih *et al.* (2009) and the IRRI Standard Evaluation System for Rice (IRRI, 2002). Plant survival was assessed 21 days after de-submergence. A plant was considered to have survived if it exhibited active regrowth, characterized by the emergence of new green leaves or tillers from the basal nodes. Survival percentage was calculated as the proportion of surviving plants relative to the total number of plants subjected to submergence in each experimental unit. For measuring % shoot elongation, the seedling length measurements were taken immediately before submergence and immediately after de-submergence. Shoot elongation (%) during submergence was calculated following formula:

$$\textit{Shoot elongation}\ (\%) = \left[\frac{(\textit{Height after submergence} - \textit{Height before submergence})}{\textit{Height before submergence}}\right] \times 100$$

Final plant height (cm) at maturity was analysed separately as an absolute morphological trait and was not used to infer submergence-induced elongation responses. The number of tillers per plant was recorded at physiological maturity by counting all productive and non-productive tillers from tagged plants in each replicate. A panicle number per plant was determined by counting the total number of panicle-bearing tillers at maturity. Days to 50% flowering were recorded as the number of days from sowing until approximately 50% of plants in each experimental plot had exerted panicles and flowered. GY was determined on a per-plant basis at physiological maturity. All panicles from all the plants from the plots were harvested manually, sun-dried, and threshed. Grains were cleaned and weighed after air-drying. Grain weight was adjusted to a standard moisture content of 14% prior to analysis. GY per hectare (kg ha^{-1}) was estimated by extrapolating per-plot yield based on plant density at harvest.

Statistical analysis

Data from the two-year planting season were analysed using R Statistical software package version 3.6.2. The analysis used general linear models where replications and varieties were considered as fixed. Significant means were separated using Tukey's Honest Significant Difference (HSD). The data presented in the tables are combined means of the two independent trials.

Pearson's correlation coefficients were computed among all measured traits – viz. survival percentage, shoot elongation (%), days to flowering, number of tillers, number of panicles, and GY – using R software (Core Team, 2024). Correlation matrices and heatmaps were produced using the 'corrplot' package to visualize the strength and direction of relationships among traits. Correlation analysis was performed using pooled data from both single- and double-submergence treatments to examine overall trait interrelationships under submergence stress. To examine patterns of trait associations and genotype groupings, a principal component analysis (PCA) was conducted on standardized mean trait values. The first two principal components (PC1 and PC2) were used for visualization in a biplot. Hierarchical clustering of genotypes was applied to the PCA scores to identify distinct response groups, and the clusters were overlaid on the biplot using the 'factoextra' package in R.

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Table 2. Analysis of variance showing the effect of single- and double-submergence stresses on 15 rice varieties.

Source of variation	d. f	Survival (%)	Shoot elongation (%)	Days to 50% flowering	Plant height (cm)	Tiller number	Panicle number	Yield (kg h^{-1})
Rep (R)	2	39.9ns	58ns	16ns	101ns	1.1ns	0.1ns	0.02ns
Year (Y)	1	54.4ns	2608ns	2250ns	1440ns	0.3ns	1.7ns	0.01ns
Genotype (G)	14	8645.1**	4576**	6835**	2480**	71.6**	29.7**	9.6**
Treatment (T)	1	1312.1**	213485**	90757**	87285**	406.2**	128.4**	18.8**
G X T	14	467.6**	18087**	7030**	3586**	16.2**	4.9**	1.1**
Error	30	19.2	33	13	224	0.5	0.4	0.02

**Significant at 1% probability level, *significant at 5% probability level, NS not significant.

Table 3. Percentage mean survival under two different submergence stress conditions.

Variety	Single submergence (%)	Double submergence (%)	Survival difference (%)
Samba Masuri-Sub1	77.5ab	94.1ab*	16.5
CHAKURAGI	35.8d	0*	−35.8
FARO 44	15.8f	0*	−15.8
FARO 52	27.5fg	0*	−27.5
FARO 57	9.1gh	0*	−9.2
FARO 60	15.0fg	0*	−15
FARO 66	75.0bc	90.7bc*	15.7
FARO 67	83.3a	96.5a*	13
IR64-Sub1	75.8b	94.1ab*	18.3
Ladanci	5.0h	0*	−5
NERICA-L-52	14.2fg	0*	−14.2
R84196	29.2e	0*	−29.2
Swarna-Sub1	84.2a	89.9c*	5.7
TOS 6454	77.5bc	76.7d#	−0.8
UPIA 3	18.3f	0*	−18.3
Mean	42.9	36.1	−6.8
SD	31.5	46	14.5
SE	8.1	11.9	3.8
CV	73.5	127.4	53.9

The sign '*' indicates significant differences between single and double submergence stress treatments, while '#' indicates no significant differences between single- and double-submergence stress treatments at a 5% probability level. The total number of germinated seedlings in each plot was counted at the start of submergence stress treatments and at the end of the recovery to calculate the % of seedlings that survived in each plot. Survival difference (%) is calculated as the difference between double- and single-submergence treatments. Means followed by the same letter along the same treatment column are not significantly different from one another at 5% probability level.

Results

Analysis of variance for different traits of 15 rice genotypes evaluated under submergence stress conditions indicated that there was no significant effect due to replication and season of planting in all traits studied (Table 2). Genotype, submergence stress treatment, and their interaction were significantly different ($P < 0.01$) for all traits (Table 2).

The survival percentage declined significantly for submergence-sensitive non-Sub1 genotypes under double submergence stress compared to single submergence stress (Table 3). All non-SUB1 lines had 0% survival after double submergence treatment, indicating that these varieties failed to recover from the initial exposure. In contrast, submergence-tolerant Sub1 varieties such as FARO 66, FARO 67, IR-64-Sub1, Samba Masuri-Sub1, and Swarna-Sub1 exhibited high survival rates under both single- and double-submergence conditions (Table 3). The survival rates of these Sub1 varieties increased by 5.7%–18.2% under the double-submergence stress treatment compared to single-submergence treatment (Table 3). However, the survival % of submergence-

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Table 4. Seedling shoot elongation (%) of 15 rice varieties under two different submergence stress conditions.

Variety	Single submergence (%)	Double submergence (%)
Samba Masuri-Sub1	3.3e	5.5b#
CHAKURAGI	22.7b	−35.3*
FARO 44	13.6cd	−34.5*
FARO 52	16.8c	−31.1*
FARO 57	18.5bc	−30.9*
FARO 60	21.4bc	−39.6*
FARO 66	2.2e	6.7b*
FARO 67	4.1e	8.9ab*
IR64-Sub1	2.9e	6.2b*
Ladanci	−2.3	−33.4*
NERICA-L-52	62.8a	−34.9*
R84196	−5.8	−42.8*
Swarna-Sub1	3.4e	2.3b#
TOS 6454	11.7d	12.5a#
UPIA 3	8.2de	−40.1*
Mean	12.2	−18.7
SD	18.1	22.1
SE	4.7	5.7
CV	143.1	−117.7

The sign '*' indicates significant differences between single and double submergence stress treatments, while '#' indicates no significant differences between single- and double-submergence stress treatments at a 5% probability level. For measuring % shoot elongation, the seedling length measurements were taken immediately before submergence and immediately after de-submergence. % elongation under submergence treatment was calculated considering shoot length before submergence as 100%. The values are means of 20 recorded observations. Means followed by the same letter along the same treatment column are not significantly different from one another at the 5% probability level.

tolerant landrace TOS 6454 remained similar under both single- and double-submergence treatments.

The shoot elongation response, a key adaptation mechanism under submergence, varied widely among varieties. Under single-submergence stress, NERICA-L-52 recorded the highest shoot elongation (62.26%), whereas FARO 66 exhibited minimal elongation (2.21%) (Table 4). The Sub1 varieties maintained lowest % elongation under single-submergence treatment, while the non-Sub1 varieties exhibited significantly higher % elongation compared to all Sub1 varieties. In the double-submergence condition, shoot elongation was significantly reduced in all non-Sub1 varieties, all exhibiting negative growth values (Table 4). Notably, all Sub1 varieties maintained a low elongation response across treatments. The submergence-tolerant landrace TOS 6454 maintained similar % elongation rates under both single- and double-submergence stress, however, the elongation % of TOS 6454 was significantly higher than all Sub1 varieties under both single- and double-submergence stress treatments (Table 4).

Plant height was significantly affected by both submergence stress treatments. Under single-submergence stress, Ladanci had a relatively shortest plant height (40.67 cm), and FARO 60 recorded the highest plant height (134.67 cm) (Table 5). The Sub1-varieties exhibited lower plant heights compared to the non-Sub1 varieties under single-submergence stress except for FARO 66 and FARO 67. In the double-submergence condition, plant height for non-Sub1 lines could not be recorded, as none of them survived. Plant height was significantly reduced in all Sub1 genotypes under double-submergence stress compared to the single-submergence treatment (Table 5). The submergence-tolerant landrace TOS 6454 also exhibited a significant decline in plant height under double-submergence stress compared to single-submergence stress. However, plant height of TOS6454 was significantly higher than all Sub1 varieties under both stress treatments (Table 5).

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Table 5. Plant height of 15 rice varieties after-submergence stress in the field.

Variety	Single submergence (cm)	Double submergence (cm)
Samba Masuri-Sub1	70.9f	59.1d*
CHAKURAGI	86e	–
FARO 44	92.3de	–
FARO 52	119.3c	–
FARO 57	127.7b	–
FARO 60	134.7a	–
FARO 66	80e	68.5c*
FARO 67	88.5de	80.5b*
IR64-Sub1	61.7g	60.8d#
Ladanci	40.7h	–
NERICA-L-52	123bc	–
R84196	95d	–
Swarna-Sub1	66.3fg	37.4e*
TOS 6454	117c	103.6a*
UPIA 3	84.7e	–
Mean	92.5	27.3
SD	27.2	37.1
SE	7.1	9.6
CV	29.4	135.9

The sign '*' indicates significant differences between single- and double-submergence stress treatments, while '#' indicates no significant differences between single- and double-submergence stress treatments at the 5% probability level. Plant height was measured by measuring scale at maturity from the soil surface to the top of the panicle of the longest tiller in the hill. The values are means of 20 recorded observations. Means followed by the same letter along the same treatment column are not significantly different from one another at the 5% probability level.

Under single-submergence stress conditions, Ladanci recorded the longest days to flowering 144 days, while FARO 44 had the shortest days to flowering 113 days (Figure 1a). The days to flowering increased significantly under double-submergence stress treatment for TOS 6454 and all Sub1 varieties compared to single-submergence treatment except for FARO 66 (Figure 1a). Under double-submergence stress condition, Swarna-Sub1 had the longest flowering days of 153 days, while FARO 66 have the least flowering days of 124 (Figure 1a).

All Sub1 varieties maintained significantly higher tillers and panicle numbers compared to the non-Sub1 varieties except for FAR0 52 and FARO 57 (Table 6). Under single-submergence stress, Swarna-Sub1 maintained a relatively high tiller number (12.2) and panicle count (7.61), whereas susceptible non-Sub1 genotypes such as Ladanci and FARO 44 had lowest tillers and panicles (Table 6). Under double-submergence stress all Sub1 varieties maintained similar numbers of tillers and panicles as under single-submergence treatment except for Samba Masuri-Sub1 and TOS 6454, which exhibited a significant decline in numbers of tillers and panicles under double-submergence stress compared to single-submergence stress (Table 6).

Submergence-tolerant Sub1 varieties yielded higher than the non-Sub1 varieties under single-submergence treatment (Figure 1b). There was a significant decline in GY in all genotypes under double-submergence stress compared to the single submergence (Figure 1b). The highest yielding submergence-tolerant genotypes with Sub1 gene, FARO 66, FARO 67, Swarna-Sub1, IR 64-Sub1, Sambha Masuri-Sub1 and TOS 6454 all showed a significant decline in yield under double-submergence stress compared to single-submergence stress (Figure 1b). For all other non-Sub1 susceptible genotypes, no GY could be recorded after double-submergence stress as none of them survived double-submergence stress.

Correlation analysis revealed strong positive associations between yield and key yield components (Figure 2). GY was highly correlated with survival ($r = 0.86$), panicle number ($r = 0.73$), and tiller number ($r = 0.73$), indicating that both plant survival and sink-related traits contributed substantially to yield performance under submergence conditions. Panicle number was strongly associated with tiller number ($r = 0.95$), reflecting the close developmental linkage

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

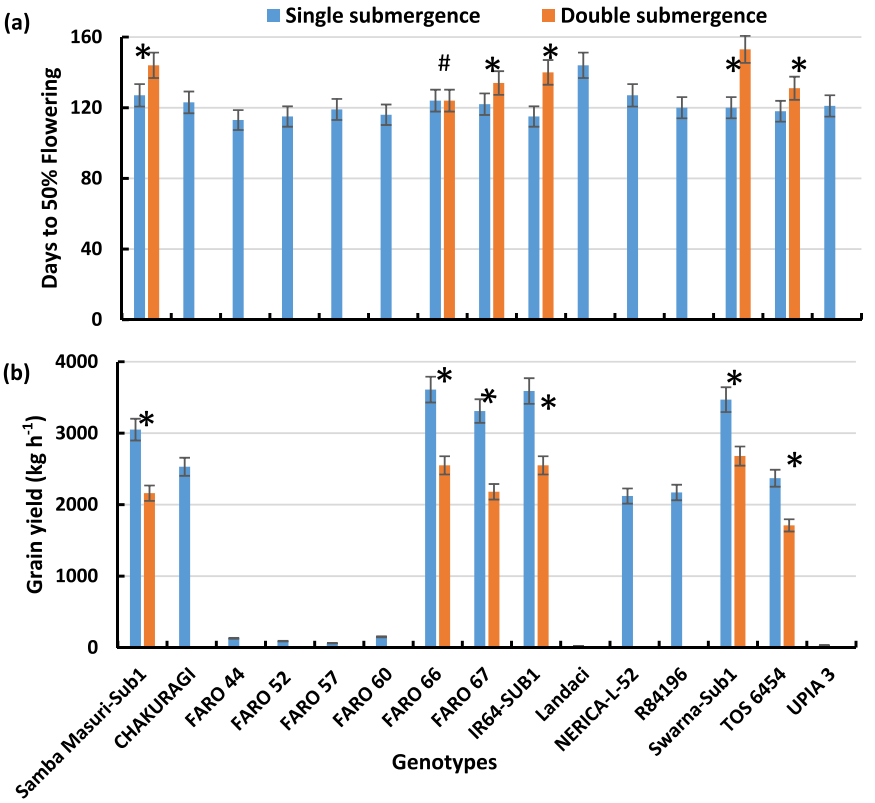


Figure 1. Days to 50% flowering (a) and grain yield (b) of 15 rice genotypes evaluated under different submergence stress treatments. Days to 50% flowering were recorded when all plants in a plot show at least 50% flowering. Plot yields were measured in grams from three replicates and converted to kg h^{-1}. Error bars indicate standard error in the measurement ($n = 3$). The sign '*' indicates significant differences between single- and double-submergence stress treatments for same genotype at 5% probability level.

between these traits. Flowering time (FLW) also showed moderate-to-strong positive correlations with yield ($r = 0.65$) and other traits. In contrast, shoot elongation exhibited comparatively weaker associations with GY ($r = 0.35$) and survival percentage ($r = 0.36$), suggesting a limited direct contribution of elongation to productivity in the genotypes used in this study (Figure 2). PCA supported these relationships. The first principal component (PC1), explaining 74.2% of the total variation, was primarily associated with GY, survival, tiller number, and panicle number, indicating that these traits collectively define the major axis of variation among genotypes (Figure 3). The second principal component (PC2) explaining 13.8% of total variation, was largely influenced by shoot elongation, which was oriented orthogonally to yield and yield components. This separation indicates that elongation represents an independent response dimension that is not closely aligned with yield performance under submergence stress in the genotypes used in this study.

Discussion

This present study provides limited evidence for acclimation to repeated submergence stress, and this response appears to be restricted to plant survival in a subset of genotypes, particularly those carrying the *Sub1* locus. While some genotypes exhibited improved survival following repeated

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Table 6. Tiller and panicle number of 15 rice varieties evaluated under submergence stress treatments in the field.

	Tiller		Panicle	
Variety	Single submergence (number)	Double submergence (number)	Single submergence (number)	Double submergence (number)
Samba Masuri-Sub1	10.3ab	7.3bc*	6.5ab	4.5b*
CHAKURAGI	4.8cd	–	2.5cd	–
FARO 44	6c	–	3cd	–
FARO 52	9.7b	–	6ab	–
FARO 57	10.3ab	–	5.5b	–
FARO 60	6.7c	–	3.5c	–
FARO 66	10.1ab	11ab#	6.2ab	7.5a#
FARO 67	8.9bc	8.6b#	5.5b	6.1a#
IR64-Sub1	10.8ab	11.9a#	6.2ab	6a#
Ladanci	3.2d	–	1.6d	–
NERICA-L-52	4.5cd	–	2.5cd	–
R84196	4.8cd	–	2.3cd	–
Swarna-Sub1	12.2a	11.1ab#	7.6a	6.9a#
TOS 6454	10.8ab	5.4c*	4.8bc	3.9b#
UPIA 3	4.7cd	–	3.2c	–
Mean	7.9	3.7	4.5	2.3
SD	3.1	4.9	1.9	3.1
SE	0.8	1.3	0.5	0.8
CV	38.6	133.4	43.2	132.4

The sign '*' indicates significant differences between single- and double-submergence stress treatments, while '#' indicates no significant differences between single- and double-submergence stress treatments at the 5% probability level. The total number of the tillers and panicles was counted on 20 hills in each plot, and the values given are means of 20 recorded observations. Means followed by the same letter along the same treatment column are not significantly different from one another at the 5% probability level.

submergence, this effect did not translate into improvements in key productivity traits, including tiller number, panicle number, or GY. The correlation and multivariate analyses further support this distinction, showing that although survival is positively associated with yield formation, it is more strongly driven by the maintenance of tiller and panicle number. Therefore, the observed response is best interpreted as a partial acclimation effect, confined to the plant's ability to withstand stress, rather than a comprehensive adaptive advantage affecting overall plant growth and performance. This suggests that the *Sub1*-mediated quiescence strategy may enhance survival under repeated stress but may not prevent the downstream penalties on growth and reproductive development that ultimately determine yield. This could be attributed to the fact that rice plants rely on stored carbohydrate reserves for survival under submerged conditions. During the first submergence event, these reserves are depleted, and while some varieties manage to survive a second submergence, they may lack sufficient energy for post-submergence recovery and reproductive growth. This aligns with previous studies that highlight the importance of carbohydrate availability in submergence tolerance (Das *et al.*, 2009; Singh *et al.*, 2017).

The role of shoot elongation in submergence tolerance is well known (Sakagami *et al.*, 2013). In the present study, some varieties exhibited a higher degree of elongation compared to others (Table 4). Excessive shoot elongation can be detrimental, as it leads to energy depletion. *Sub1* varieties such as Swarna-Sub1 and Samba Masuri-Sub1, which maintained a low elongation rate, demonstrated the well-documented quiescence strategy associated with the *Sub1* gene. This response minimizes energy expenditure, allowing plants to survive under prolonged submergence stress. Conversely, varieties with excessive shoot elongation, such as NERICA-L-52, experienced greater stress post-submergence due to carbohydrate exhaustion, which clearly explains their lower yield performance after recovery. Interestingly, the submergence-tolerant landrace TOS 6454 (Agbeleye *et al.*, 2019) exhibited significantly higher elongation compared to varieties with *Sub1* locus (Table 4), but that elongation was less than all non-*Sub1* varieties. TOS 6454 is known to carry an additional epistatic *Sub2* QTL on chromosome 2 in addition to *Sub1* locus on

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

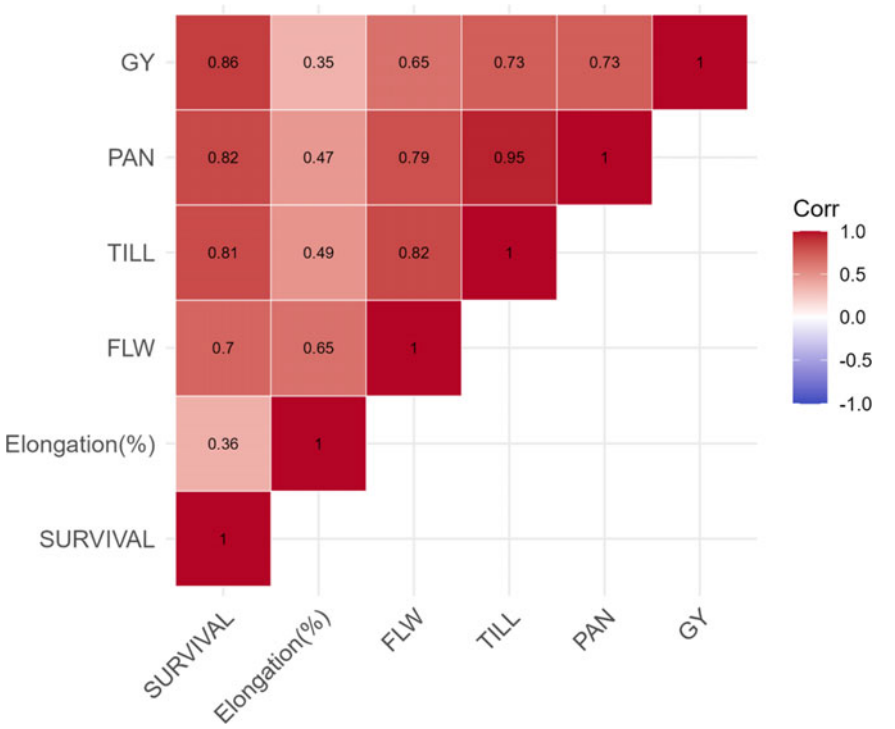


Figure 2. Pearson's correlation heat map showing relationships among survival percentage, shoot elongation, flowering time, and yield-related traits of rice genotypes evaluated under submergence stress. Data from single- and double-submergence treatments were pooled to examine overall trait interrelationships under submergence conditions. Color intensity represents the strength and direction of correlations. GY = grain yield; PAN= number of panicles; TILL = number of tillers; FLW = days to 50% flowering; Elongation (%) = seeding elongation % under submergence; SURVIVAL = survival %; Corr = correlation coefficient.

chromosome 9 (Akintayo *et al.*, 2023). The interaction between *Sub1* and *Sub2* may have led to elongation resulting in partial quiescence in TOS 6454 under submergence stress.

The delay in days to flowering observed in all varieties after double submergence stress suggests that reproductive development is particularly sensitive to flooding. This is consistent with reports by Septiningsih *et al.* (2009) and, Sarkar and Bhattacharjee (2011), who reported that submergence stress alters hormonal balances, particularly ethylene and gibberellin levels, leading to delays in panicle initiation and flowering. Delayed flowering may have negatively impacted grain filling duration, leading to yield losses despite successful survival as observed in this study (Figure 1a, b).

The fewer tiller and panicle numbers under double-submergence stress further explain the lack of yield advantage in acclimated plants. The ability of rice plants to recover from submergence depends not only on survival but also on their ability to restore tiller production. However, repeated submergence appears to cause cumulative damage, preventing effective tiller regeneration. This finding is supported by studies that indicate submergence stress suppresses hormonal activity, which is crucial for tiller bud initiation in rice (Fukao and Bailey Serres 2008; Zha *et al.*, 2022). It is well known that submergence-tolerant genotypes with *Sub1* locus have the capacity to recover faster and resume normal growth, leading to high numbers of tillers; however, that capacity is greatly compromised when the stress duration is longer than 14 days (Singh *et al.*, 2014). Maintaining high productive tillering is reported to be essential for yield maintenance in

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

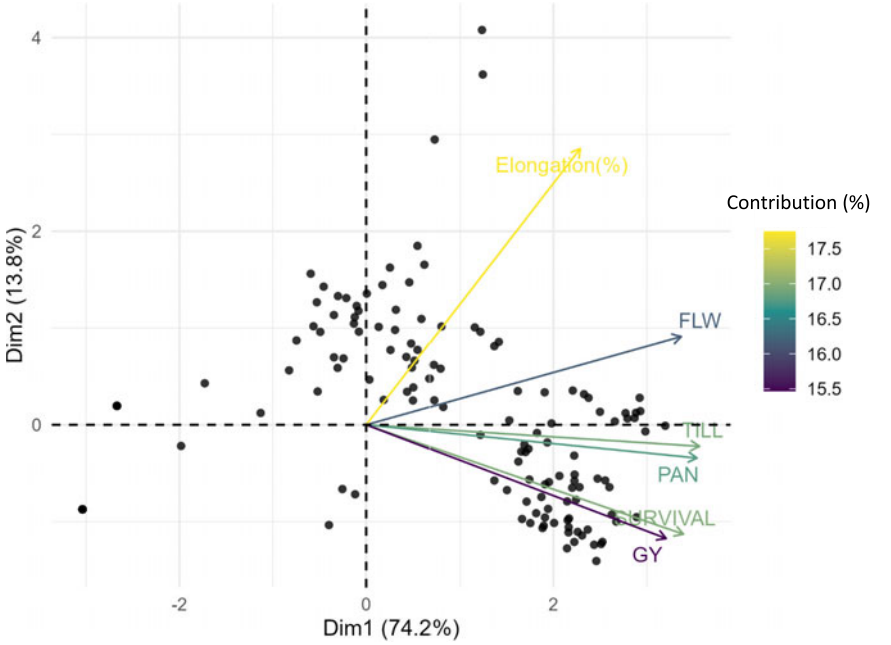


Figure 3. Principal component analysis (PCA) biplot illustrating the multivariate relationships among survival, growth, phenology, and yield-related traits of rice genotypes under submergence stress. Trait vectors indicate variable loadings, while points represent individual observations. The first two principal components (PC1 and PC2) explain most of the total variation. GY = grain yield; PAN = number of panicles; TILL = number of tillers; FLW = days to 50% flowering; Elongation (%) = seeding elongation % under submergence; SURVIVAL = survival %; Dim1 = principal component 1; Dim2 = principal component 2.

rice in other long-term flooding stresses like stagnant flooding also (Semwal *et al.*, 2025; Semwal *et al.*, 2026). Repeated submergence may limit this ability of recovery and growth in *Sub1* varieties.

Despite some improvement in survival, GY remained significantly lower under double-submergence stress, indicating high survival under submergence stress alone does not enhance yield potential. The reduction in yield under double-submergence stress could be attributed to several physiological constraints: (i) prolonged submergence may induce chlorophyll degradation resulting in reduced photosynthetic efficiency and limiting post-submergence recovery (Sone and Sakagami, 2017); (ii) submergence stress may have led to nutrient leaching and depletion of essential elements such as nitrogen, phosphorus, and potassium from the soil which are vital for grain development (Phukan *et al.*, 2024); (iii) prolonged submergence and post-submergence stress can induce spikelet sterility, reducing the number of filled grains per panicle (Behera *et al.*, 2019); and (iv) submergence-induced oxidative stress could lead to cell and tissue damage resulting in insufficient recovery (Kawano *et al.*, 2002).

The combined correlation and multivariate analyses indicate that GY under submergence stress is strongly associated with survival and yield-component traits, particularly tiller and panicle number (Figure 2). The close alignment of these traits along the primary axis of variation (PC1) suggests that yield formation is predominantly governed by the plant's ability to maintain viable tillers and reproductive structures following stress exposure (Figure 3). While survival showed a strong positive correlation with yield, its effect appears to be indirect, likely mediated through the maintenance of tiller and panicle number rather than acting as a sole determinant of productivity. Similar results have been reported in earlier study using *Sub1* varieties (Singh *et al.*, Singh *et al.*, 2014). In contrast, shoot elongation exhibited weak

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

correlations with yield and survival and was largely separated along the second principal component (Figure 3), indicating a distinct physiological response that does not directly translate into yield advantage in this study. This pattern suggests that elongation responses under submergence may reflect an adaptive strategy that is functionally independent of yield formation. Overall, these results suggest that multiple trait interactions, rather than any single trait, underpin yield performance under submergence stress, with survival and yield components playing a central role, while elongation contributes less directly to final productivity in the genotypes used in this study.

It is acknowledged that the cumulative submergence duration differed between treatments; however, this design was deliberate to reflect natural flooding recurrence rather than controlled equal-duration stress. Moreover, the plants underwent a recovery phase between the two stress events, and therefore the double-submergence treatment should not be considered a simple extension of the total submergence period. Instead, this regime represents a *priming–recovery–stress* sequence, conceptually like acclimation models described for drought, salinity, and heat stresses. Nevertheless, because the repeated-submergence treatment involved a greater cumulative duration of flooding than the single-submergence treatment, the observed differences cannot be unequivocally attributed to physiological acclimation or priming alone. It is possible that the responses reflect the combined effects of repeated exposure and cumulative stress intensity. Interestingly, despite a longer cumulative exposure, several *Sub1* genotypes exhibited higher survival under the double-submergence regime. Therefore, our results should be interpreted as evidence consistent with a limited, survival-specific acclimation response rather than definitive proof of stress priming. Future studies employing treatments with equivalent cumulative stress duration or alternative priming designs will be valuable for confirming the underlying mechanisms.

Together, the findings of this study suggest that yield penalties under repeated submergence are not solely a consequence of immediate stress damage or survival outcomes but arise from cumulative disruptions to plant development, particularly in tillering and reproductive processes. This highlights the importance of considering multiple trait responses when evaluating submergence tolerance and adaptation. Future breeding should prioritize genotypes that combine high survival with sustained tillering and panicle formation under repeated submergence. Emphasis should shift from survival alone to overall yield stability and post-submergence recovery capacity.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0014479726100428.

Data availability statement. The raw datasets obtained during this study are available on request from the corresponding author.

Acknowledgements. The authors would like to acknowledge the support of AfricaRice staff: Mr. Amidu Adelu, Ms. Margret Olom, Dr. Olatunde Azeez for helping in field management during this study.

Author contributions. NAS – Experiment execution, data collection, data analysis, writing original draft, writing, review and editing; MAAV – Conceptualization, writing, review and editing; EOI – writing, review and editing; VKS – Conceptualization, data analysis, writing, review and editing, Fund acquisition.

Funding statement. This research was supported by financial grants from the Gates Foundation (Grant number OPP1080832) to Africa Rice Center (AfricaRice).

Competing interests. The authors declare that there are no competing interests.

References

Agbeleye, O.A., Olubiyi, M.R., Ehirim, B.O., Shittu, A.O., Jolayemi, O.L., Adetimirin, V.O., Ariyo, O.J., Sani, K.A. and Venuprasad, R. (2019) Screening African rice (*O. glaberrima* Steud.) for tolerance to abiotic stress. III. Flooding. *SABRAO Journal of Breeding and Genetics* **51** (2), 128–150.

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Akintayo, O.T., Daniel, I.D., Shittu, A.O., Jolayemi, O.L., Semwal, V.K. and Venuprasad, R. (2023) QSub2: A novel QTL with positive epistasis with Sub1 gene enhances submergence tolerance in rice. *Crop Science* **63**, 1246–1256. https://doi.org/10.1002/csc2.20941.

Aryalekshmi, A.S., Vighneswaran, V. and Shilpa, K.S. (2021) Molecular screening of rice (Oryza sativa L.) genotypes for submergence tolerance. *Electronic Journal of Plant Breeding* **12**, 673–677. https://doi.org/10.37992/2021.1203.094.

Bailey-Serres, J., Fukao, T. and Gibbs, D.J. (2012) Making sense of low oxygen sensing. *Trends Plant Science* **17**, 129–138.

Balgah, R.A., Ngwa, K.A. and Buchenrieder, G.R. (2023) Impacts of floods on agriculture-dependent livelihoods in Sub-Saharan Africa: An assessment from multiple geo-ecological zones. *Land* **12**, 334. https://doi.org/10.3390/land12020334.

Behera, U.K., Singh, S., Sarangi, S.K. (2019) Post-Submergence nitrogen fertilizer management for enhancing rainfed lowland rice productivity in eastern India. *International Journal of Bio-Resource and Stress Management* **10**, 419–428.https://doi.org/10.23910/IJBSM/2019.10.4.2011a.

R Core Team, R. (2024) R: A language and environment for statistical computing. https://biostatistique.vetagro-sup.fr/guideRM1.pdf

Dar, M.H., Chakravorty, R. and Waza, S.A. (2017) Transforming rice cultivation in flood-prone coastal Odisha to ensure food and economic security. *Food Security* **9**, 711–722. https://doi.org/10.1007/s12571-017-0696-9.

Das, K.K., Panda, D. and Sarkar, R.K. (2009) Submergence tolerance in relation to variable floodwater conditions in rice. *Environmental and Experimental Botany* **66**, 425–434.

Fukagawa, N.K. and Zhiska, L.H (2019) Rice: Importance for global nutrition. *Journal of Nutrition Science and Vitaminology* **65**, S2–S3. https://doi.org/10.3177/jnsv.65.S2

Fukao, T. and Bailey-Serres, J. (2008) Submergence tolerance conferred by Sub1A Is mediated by SLR1 and SLRL1 restriction of gibberellin responses in rice. *Proceedings of the National Academy of Sciences USA* **105**, 16814–16819.

Gupta, B. and Shrestha, J. (2023) Abiotic stress adaptation and tolerance mechanisms in crop plants. *Frontiers in Plant Science* **14**, 1278895. https://doi.org/10.3389/fpls.2023.1278895.

IRRI. (2002) *Standard Evaluation System for Rice*, Philippines: International Rice Research Institute. http://www.knowledgebank.irri.org/images/docs/rice-standard-evaluation-system.pdf.

Ismail, A.M., Singh, U.S., Singh, S., Dar, M.H. and Mackill, D.J., 2013. The contribution of submergence-tolerant (Sub1) rice varieties to food security in flood-prone rainfed lowland areas in Asia. *Field Crops Research*, **152**,83–93. https://doi.org/10.1016/j.fcr.2013.01.007

Kawano, N., Ella, E. and Ito, O. (2002) Metabolic changes in rice seedlings with different submergence tolerance after desubmergence. *Environmental and Experimental Botany* **47**, 195–203.

Kuroha, T. and Ashikari, M. (2020) Molecular mechanisms and future improvement of submergence tolerance in rice. *Molecular Breeding* **40**, 41. https://doi.org/10.1007/s11032-020-01122-y.

Oladosu, Y., Rafii, M.Y. and Arolu, F. (2020) Submergence tolerance in rice: Review of mechanism, breeding and, future prospects. *Sustainability* **12**, 1632. https://doi.org/10.3390/su12041632.

Phukan, U.J., Jindal, S. and Laldinsangi, C. (2024) A microscopic scenario on recovery mechanisms under waterlogging and submergence stress in rice. *Planta* **259**, 9. https://doi.org/10.1007/s00425-023-04285-y.

Reed, C., Anderson, W. and Kruczkiewicz, A. (2022) The impact of flooding on food security across Africa. *Proceedings of the National Academy of Sciences USA* **119**, 2119399119.

Sakagami, J.-I., Yukiko, J. and Chiharu, S. (2013) Complete submergence escape with shoot elongation ability by underwater photosynthesis in African rice, Oryza glaberrima Steud. *Field Crops Research* **152**, 17–26.

Sarkar, R.K. and 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. https://doi.org/10.1007/s12284-011-9065-z.

Seck, P.A., Diagne, A. and Mohanty, S. (2012) Crops that feed the world 7: Rice. *Food Security* **4**, 7–24. https://doi.org/10.1007/s12571-012-0168-1.

Semwal, V.K., Afeez, S., Bhadmus, O.A., Okanlawon, J. and Venuprasad, R. (2026) Unveiling stagnant flooding tolerance in lowland NERICAs: Genomic insights and breeding prospects. *Theoretical and Applied Genetics* **139**, 27 https://doi.org/10.1007/s00122-025-05129-x.

Semwal, V.K., Bhadmus, O.A., Afeez, S. and Venuprasad, R. (2025) Characterization of *Oryza glaberrima* derived genetic resources for stagnant flooding tolerance in interspecific rice pre-breeding populations. *Plant Genetic Resources: Characterization and Utilization*, **24**, 47–53 https://doi.org/10.1017/S1479262125100269.

Septiningsih, E.M., Pamplona, A.M., Sanchez, D.L. (2009) Development of submergence-tolerant rice cultivars: The Sub1 locus and beyond. *Annals of Botany* **103**, 151–160. https://doi.org/10.1093/aob/mcn206.

Singh, A., Septiningsih, E.M. and Balyan, H.S. (2017) Genetics, physiological mechanisms and breeding of flood-tolerant rice (Oryza sativa L.). *Plant and Cell Physiology* **58**, 185–197. https://doi.org/10.1093/pcp/pcw206.

Singh, S., Mackill, D.J. and Iamail, A.M. (2014) Physiological basis of tolerance to complete submergence in rice involves genetic factors in addition to the Sub1 Gene. *AOB Plants* https://doi.org/10.1093/aobpla/plu060.

Sone, C. and Sakagami, J.I. (2017) Physiological mechanism of chlorophyll breakdown for leaves under complete submergence in rice. *Crop Science* **57**, 2729–2738. https://doi.org/10.2135/cropsci2016.10.0884.

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press

Tamang, B.G. and Fukao, T. (2015) Plant adaptation to multiple stresses during submergence and following desubmergence. *International Journal of Molecular Sciences* **16**, 30164–30180. https://doi.org/10.3390/ijms161226226.

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

Xu, K., Xu, X. and Ronald, P.C. (2000) A high-resolution linkage map of the vicinity of the rice submergence tolerance locus Sub1. *Molecular and General Genetics* **263**, 681–689. https://doi.org/10.1007/s004380051217.

Yuan, S., Saito, K. and van Oort, P.A. (2024) Intensifying rice production to reduce imports and land conversion in Africa. *Nature Communications* **15**, 835. https://doi.org/10.1038/s41467-024-44950-8.

Zha, M., Zhao, Y. and Wang, Y. (2022) Strigolactones and cytokinin interaction in buds in the control of rice tillering. *Frontiers in Plant Science* **13**, 837136. https://doi.org/10.3389/fpls.2022.837136.

Cite this article: Salaudeen NA, Ayo-Vaughan MA, Idehen EO, and Semwal VK (2026). Repeated submergence stress impairs yield despite improved survival in rice. *Experimental Agriculture*. https://doi.org/10.1017/S0014479726100428

https://doi.org/10.1017/S0014479726100428 Published online by Cambridge University Press