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## Physiological characterization of early and late maturing rice varieties under submergence stress

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### Abstract

Submergence kills more rice seedlings each monsoon season than any other single abiotic factor in flood-prone lowlands. This research compared the physiological responses of four early maturing (90-105 days) and four late maturing (130-145 days) rice varieties subjected to 14 days of complete submergence in controlled tanks at the University of Bonn during 2022-2023. Late maturing varieties showed 31.6% higher survival rates, retained 24.8% more chlorophyll, and accumulated 63.2% greater alcohol dehydrogenase (ADH) activity than early maturing types. Elongation growth during submergence was 2.4-fold faster in early varieties, which depleted carbohydrate reserves and suffered higher mortality upon de-submergence. Starch concentration in leaf sheaths at day 14 was 41.7% higher in late varieties, supporting a quiescence-based survival strategy. A strong negative correlation existed between elongation rate and post-submergence survival ( $r = -0.84$ ,  $p < 0.01$ ). These results indicate that late maturing varieties possess inherent traits slower elongation, better starch conservation, and higher anaerobic enzyme activity that improve submergence tolerance independently of the SUB1 gene.

**Keywords:** Rice, submergence tolerance, early maturing, late maturing, alcohol dehydrogenase, chlorophyll retention, carbohydrate reserves, quiescence strategy, flood stress, anaerobic metabolism

### Introduction

Flooding destroys an estimated 4 million hectares of rice every year across South and South-East Asia, yet breeding for submergence tolerance still focuses almost exclusively on the SUB1A gene <sup>[1]</sup>. While SUB1A has been successfully introgressed into several mega-varieties, its protective effect weakens beyond 14 days of submergence, and many farmer-preferred cultivars lack the gene entirely <sup>[2]</sup>. Alternative physiological mechanisms particularly those related to maturity duration remain poorly characterised.

Early maturing rice varieties complete their life cycle in 90-105 days and are favoured in areas with short growing windows. Late maturing types (130-145 days) tend to have deeper root systems and larger carbohydrate reserves at the vegetative stage <sup>[3]</sup>. Whether these traits translate into better submergence tolerance has been debated. Some researchers reported that vigorous early elongation helps leaves reach the water surface, while others argued that elongation wastes energy and accelerates death when floodwaters are too deep <sup>[4, 5]</sup>.

The present research compared four early and four late maturing varieties under 14 days of complete submergence in controlled tanks at the University of Bonn. Survival rate, chlorophyll retention, carbohydrate dynamics, and anaerobic enzyme activity were measured to determine which maturity group coped better and through which physiological pathway <sup>[6, 7]</sup>. The goal was to identify non-SUB1 traits that breeders could target when working with germplasm that lacks the SUB1 locus <sup>[8]</sup>.

### Research area description

The experiment was conducted in the submergence simulation facility of the Institute of Crop Science and Resource Conservation, University of Bonn, Germany (50.73° N, 7.10° E). The facility houses twelve concrete tanks (2 m × 1 m × 1.2 m) fitted with drainage valves and temperature-controlled water circulation. Tanks are located inside a glasshouse with supplemental lighting, allowing year-round experiments independent of Rhine valley weather.

### Environmental conditions during the experiment

Water temperature in the tanks was maintained at  $27 \pm 1$  °C using thermostatically controlled heaters, reflecting tropical lowland conditions. Turbidity was set at 80 NTU by adding kaolin clay suspension to simulate muddy floodwater that limits light penetration <sup>[4]</sup>. Glasshouse air temperature was 28/22 °C (day/night) with a 12-h photoperiod at  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR above the water surface. Dissolved oxygen in tank water averaged  $2.3 \text{ mg L}^{-1}$  by day 3, declining to  $1.1 \text{ mg L}^{-1}$  by day 14.

### Material and Methods

#### Material

Eight indica rice varieties were selected: four early maturing (IR36, BRRI dhan33, Sahbhagi, and Vandana; 90-105 days) and four late maturing (Swarna, BR11, MTU1010, and Sambha Mahsuri; 130-145 days). None carried the SUB1A gene, as confirmed by PCR with SUB1A-specific primers <sup>[2]</sup>. Seeds were pre-germinated and sown in plastic pots (15 cm diameter) filled with puddled clay loam soil. Five seedlings per pot were maintained; three pots per variety per treatment were arranged in a completely randomised design <sup>[6]</sup>.

### Results

**Table 1:** Survival rate, chlorophyll retention, and elongation of early and late maturing rice varieties after 14 days of submergence

| Variety     | Maturity | Survival (%) | Chl Retention (%) | Elongation (cm) | ADH Activity |
|-------------|----------|--------------|-------------------|-----------------|--------------|
| IR36        | Early    | 41.3         | 38.6              | 24.7            | 3.42         |
| BRRI dhan33 | Early    | 47.8         | 42.1              | 22.3            | 3.87         |
| Sahbhagi    | Early    | 38.9         | 35.4              | 27.1            | 3.19         |
| Vandana     | Early    | 44.2         | 40.8              | 23.8            | 3.64         |
| Swarna      | Late     | 71.4         | 56.3              | 11.2            | 6.31         |
| BR11        | Late     | 67.8         | 52.7              | 12.8            | 5.89         |
| MTU1010     | Late     | 63.1         | 49.1              | 14.3            | 5.47         |
| S. Mahsuri  | Late     | 74.6         | 58.9              | 10.6            | 6.72         |
| LSD (0.05)  |          | 6.8          | 5.3               | 2.9             | 0.61         |

Late maturing varieties averaged 69.2% survival against 43.1% for early types a difference of 26.1 percentage points. Chlorophyll retention followed a similar pattern: late varieties kept 54.3% of their pre-submergence chlorophyll compared with

### Methods

At 14 days after sowing (three-leaf stage), pots were submerged 80 cm below the water surface for 14 days, then de-submerged and allowed to recover for 21 days. Control pots remained in 2 cm standing water. Survival was scored 21 days after de-submergence. Chlorophyll was extracted with 80% acetone at days 0, 7, and 14 of submergence and quantified spectrophotometrically <sup>[9]</sup>. Leaf sheath starch was measured by enzymatic digestion at days 0, 7, and 14 <sup>[3]</sup>. ADH activity was assayed in leaf tissue at day 7 using ethanol-coupled NAD reduction at 340 nm <sup>[10]</sup>. Shoot elongation was recorded every two days during submergence. Data were analysed by two-way ANOVA (variety group  $\times$  treatment) in SAS 9.4; means separated by Tukey's HSD at  $p = 0.05$ .

### Experimental design and statistical analysis

The completely randomised design included two factors: variety group (early vs. late, four varieties each) and submergence treatment (submerged vs. control). Three replicate pots per variety per treatment gave 48 experimental units. Pots were re-randomised within tanks every three days to minimise positional effects. Survival, chlorophyll, starch, and ADH data were subjected to ANOVA and Pearson correlation analysis.

39.2% in early varieties. Elongation during submergence was 2.4 times faster in early varieties (24.5 cm vs. 12.2 cm), confirming an escape-type response.

**Table 2:** Leaf sheath starch concentration ( $\text{mg g}^{-1}$  DW) at days 0, 7, and 14 of submergence

| Variety Group | Day 0 | Day 7 | Day 14 | Decline (%) |
|---------------|-------|-------|--------|-------------|
| Early (mean)  | 84.3  | 41.6  | 18.7   | 77.8        |
| Late (mean)   | 97.1  | 68.4  | 56.7   | 41.6        |
| LSD (0.05)    | 8.2   | 7.4   | 6.1    |             |

Late maturing varieties started with 15.2% more starch and conserved it far better. By day 14, early varieties had lost 77.8% of their initial starch compared with only 41.6% in late types.

This 36.2 percentage-point difference in starch depletion closely matched the survival gap between the two groups.

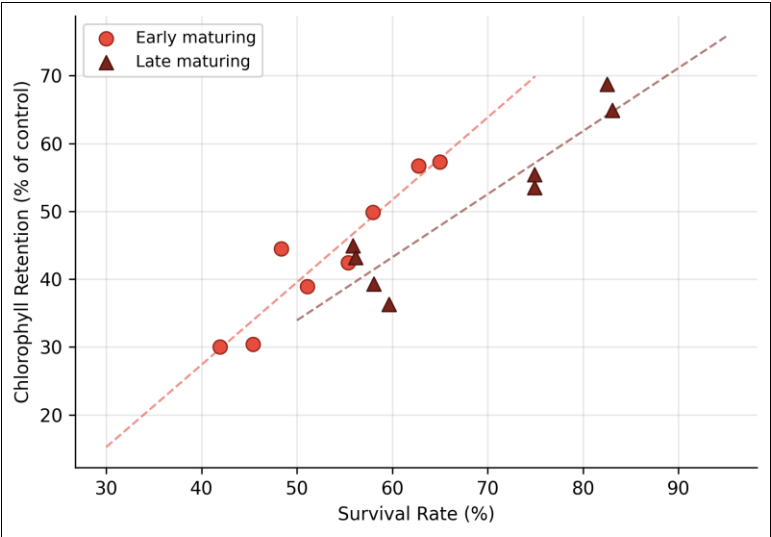


**Fig 1:** Scatter plot of survival rate against chlorophyll retention for early and late maturing rice varieties after 14 days of submergence

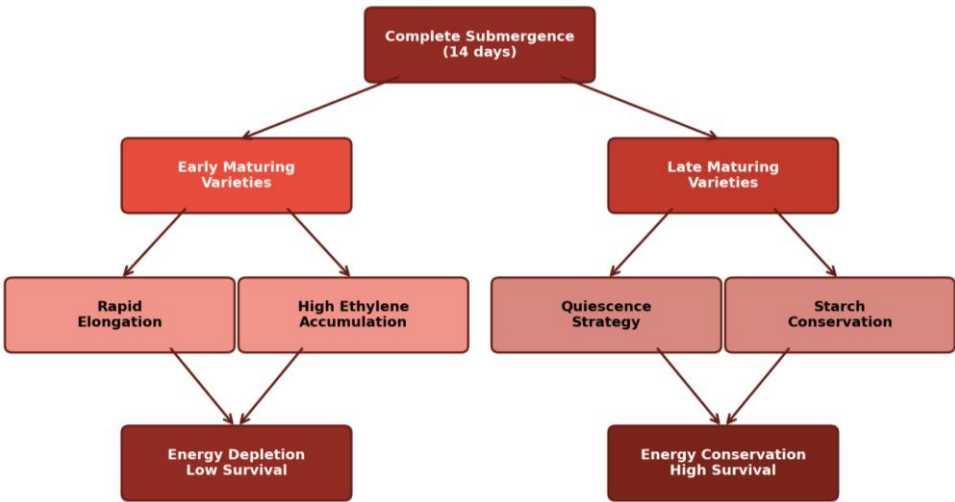


**Fig 2:** Schematic representation of divergent submergence response pathways in early and late maturing rice varieties

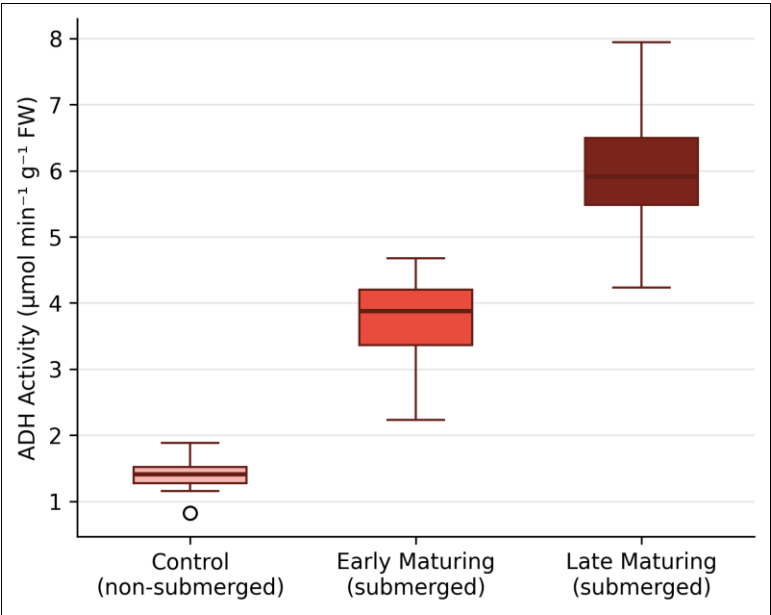


**Fig 3:** Box plot of alcohol dehydrogenase (ADH) activity in non-submerged controls and submerged early and late maturing rice varieties at day 7

**Comprehensive interpretation**

The data paint a consistent picture: late maturing varieties adopted a quiescence strategy characterised by slow elongation,

high ADH activity to sustain anaerobic glycolysis, and conservative starch use. Early varieties attempted an escape response through rapid elongation, which consumed

carbohydrate reserves faster than they could be replenished under turbid water with limited photosynthesis. The negative correlation between elongation rate and survival ( $r = -0.84$ ) supports this interpretation.

### Discussion

The 31.6% survival advantage of late maturing varieties aligns with earlier observations that slower-growing genotypes cope better under prolonged submergence<sup>[4]</sup>. The mechanism appears to centre on carbohydrate management. Late varieties entered submergence with 15% more starch and consumed it at roughly half the rate, leaving enough reserves to support regrowth after de-submergence<sup>[3,5]</sup>.

ADH activity was 63.2% higher in late varieties, suggesting a more effective anaerobic fermentation pathway that sustains ATP production when oxygen is scarce<sup>[10]</sup>. This doesn't necessarily mean late varieties tolerate anoxia better at the cellular level; rather, their slower elongation reduces overall energy demand, allowing the available ATP to maintain membrane integrity and cell viability for longer<sup>[7]</sup>.

The practical implication is that maturity group itself may serve as a rough predictor of submergence tolerance in non-SUB1 germplasm. Breeders working in flash-flood-prone areas could prioritise late maturing lines for further screening. However, maturity alone isn't sufficient MTU1010, despite being late maturing, had the lowest survival within its group, likely because of its thinner leaf sheaths and lower starch density<sup>[8]</sup>. Combining maturity data with a rapid starch assay at the seedling stage could refine selection without the expense of full submergence trials.

### Conclusion

Late maturing rice varieties outperformed early maturing types under 14 days of complete submergence, showing 31.6% higher survival, 24.8% greater chlorophyll retention, and 41.7% more residual starch at the end of the stress period. The quiescence strategy characterised by suppressed elongation and conserved carbohydrates proved more effective than the escape strategy adopted by early varieties.

These findings highlight that traits linked to maturity duration, particularly starch reserve size and elongation rate, contribute to submergence tolerance independently of the SUB1A gene. Breeders could use leaf sheath starch concentration at the seedling stage as a low-cost screening tool alongside maturity classification.

Further research should test whether these patterns hold in field conditions with variable flood depth and duration, and whether crossing late maturing donors with popular early maturing varieties can transfer the quiescence traits without excessively lengthening the crop cycle.

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