PLANT SCIENCE TODAY
Vol x(x): xx–xx
https://doi.org/10.14719/pst.11416

eISSN 2348-1900

RESEARCH ARTICLE

Effects of submergence time, light and nitrate compounds on the survival of some modern rice cultivars under flooded conditions

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Received: 22 August 2025; Accepted: 16 December 2025; Available online: Version 1.0: 03 February 2026

Cite this article: Pham PN, Nguyen TDK. Effects of submergence time, light and nitrate compounds on the survival of some modern rice cultivars under flooded conditions. Plant Science Today (Early Access). https://doi.org/10.14719/pst.11416

Abstract

Flooding significantly affects rice survival due to fast oxygen depletion, and the possible use of nitrate (NO_3^-) as an alternate terminal electron acceptor to enable anaerobic metabolism remains little investigated. In particular, the efficiency of different NO_3^- compounds in increasing submergence tolerance across different rice cultivars has received little attention. Six rice cultivars-OM4900, OM6976, OM4218, IR50404, OM7347 and IR64Sub1-were tested for their flooding responses during 5-10 and 15-day submergence periods in dark conditions. Additionally, the effects of exogenous NO_3^- treatments on seedling survival were evaluated. After 5 days, IR64Sub1, OM7347 and OM4900 exhibited the highest survival rates (86, 83 and 81 %, respectively). Survival sharply decreased after 10 days, with most cultivars falling below 26 %, except OM7347 and IR64Sub1, which were reduced to 38.7 and 30.7 %, respectively. At 15 days, survival was ≤10 % for all lines. Light significantly improved survival (72.91 %) compared with dark conditions (12.31 %), and darkness induced a 142.252 % increase in soluble sugar levels, demonstrating the importance of carbohydrate reserves under hypoxia. Application of 3 mg L^{-1} calcium nitrate ($Ca(NO_3)_2$) increased survival after 10-day submergence by 47.7 % in OM4218, 53 % in OM4900, and 40 % in IR64Sub1, while silver nitrate ($AgNO_3$) stimulated shoot elongation (up to 4.42 cm). Calcium nitrate also increased soluble sugar accumulation to 2.91.5.31 mg g^{-1} dry weight (DW). Dissolved oxygen measurements showed delayed oxygen depletion under $Ca(NO_3)_2$ and elevated oxygen availability with $AgNO_3$. These results highlight the novel role of NO_3^- compounds in enhancing rice submergence tolerance and provide a foundation for further elucidation of NO_3^--mediated mechanisms of anaerobic survival.

Keywords: $AgNO_3$; $Ca(NO_3)_2$; hypoxia tolerance; IR64Sub1; nitrate

Introduction

Flooding has become a severe abiotic stress that directly affects agricultural yields, especially owing to climate change (1). Submergence restricts light penetration due to suspended sediments and dissolved organic matter and imposes partial (hypoxia) or complete (anoxia) oxygen deprivation, disrupting metabolic activity and plant growth. To cope with oxygen limitation, plants develop several adaptive traits, including hypertrophied lenticels that facilitate oxygen diffusion and the release of fermentative metabolites, extensive aerenchyma formation that improves internal O_2 transport, and adventitious roots that support nutrient uptake under prolonged inundation (2). The maintenance of non-structural carbohydrate reserves and suppression of toxic by-product accumulation are also central to flooding tolerance.

Rice (*Oryza sativa* L.), a staple crop for more than 3.5 billion people, is well adapted to waterlogged soils, yet many modern high-yielding cultivars remain vulnerable to complete submergence (3). The discovery of the SUB1A gene in the landrace FR13A and its introgression into popular varieties significantly improved tolerance through a quiescence strategy that conserves energy and limits elongation growth. However, recent studies indicate that FR13A harbors additional, unexplored genetic variation that enhances survival beyond SUB1A-mediated tolerance (4, 5), highlighting the need for complementary strategies, including physiological interventions, to improve the survival of modern cultivars, particularly those cultivated in the Mekong Delta.

Beyond inherent genetic tolerance, exogenous compounds that support metabolism under low oxygen have emerged as promising tools to mitigate flooding damage. In this context, nitrate (NO_3^-) has gained attention not only as a nitrogen nutrient but also as a functional component of hypoxia tolerance. Under low-oxygen conditions, NO_3^- can be reduced to nitrite and further to nitric oxide (NO), forming the NO_3^- nitrite (NO_2^-)-NO pathway that acts as an alternative electron sink, contributes to ATP generation via “nitrite-NO respiration”, helps regenerate NAD(P)- and buffers cytoplasmic acidosis (6). Nitrate has emerged as a promising modulator of plant survival under low-oxygen conditions. Beyond its role as a nutrient, NO_3^- participates in the NO_3^--NO_2^--NO pathway, which functions as an alternative terminal electron acceptor and contributes to proton consumption, NAD(P)- regeneration and stabilization of cytoplasmic pH during hypoxia (6, 7). Recent work demonstrates that NO_3^- or NO can enhance anaerobic respiration, adventitious root formation, mitochondrial protection, and stress signalling under waterlogging (8). Accumulating evidence shows that NO_3^- and NO signalling modulate aerenchyma formation, mitochondrial protection, antioxidant defense and energy metabolism during hypoxia and anoxia, thereby enhancing plant tolerance to waterlogging and related stresses (6). For example, NO_3^- application has recently been shown to alleviate waterlogging stress in cucumber by NO-mediated adjustments in anaerobic respiration, adventitious root formation, and NO_3^- transporter expression (8). In agricultural practice, NO_3^- is supplied predominantly as NO_3^- salts, such as calcium nitrate Ca $(NO_3)_2$, magnesium nitrate ($Mg(NO_3)_2$), and silver nitrate ($AgNO_3$). Calcium (Ca) plays key roles in membrane stability and signalling and can mitigate damage from heat, cold, and drought, while magnesium is central to chlorophyll, photosynthesis, and numerous enzyme systems (9, 10). Silver nitrate, through its effects on ethylene signalling, is widely applied to modulate plant growth, flowering, and fruit development (11). Despite these well-known agronomic functions, the extent to which these NO_3^- salts, via their NO_3^- moiety and associated ions, can act as alternative oxygen acceptors and improve plant survival under complete submergence has not been systematically examined, particularly in rice seedlings.

Given the importance of rice for food security in Asia and the vulnerability of many high - yielding varieties in the Mekong Delta to sudden flooding, there is a clear need to explore whether NO_3^- containing compounds can be exploited to enhance anaerobic survival. Building on recent advances in our understanding of submergence-tolerant rice and the NO_3^--NO_2^--NO pathway, this study addresses that gap by using $Ca(NO_3)_2$, $Mg(NO_3)_2$, and $AgNO_3$ as model NO_3^- sources. The specific objectives of this work were to: (i) assess the submergence tolerance of several widely cultivated rice varieties from the Mekong Delta across different flooding durations; and (ii) determine the extent to which exogenous application of selected NO_3^- compounds improve seedling survival, growth responses and soluble sugar status under complete submergence.

Materials and Methods

Plant materials and treatments

Six rice cultivars, including OM4900, OM4218, OM6976, OM7347, IR50404 and a submergence-tolerant IR64Sub1, were collected from Cuu Long Rice Research Institute, Can Tho, Vietnam. Rice seeds were surface-sterilized with a 2.5 % sodium hypochlorite (NaClO) solution for 15 min, then washed 5 times with distilled water. After that, the seeds were given time to germinate on Petri plates in a dark incubator at 37 °C. After three days of incubation, uniformly germinated seeds were selected and placed in plastic containers (22 cm x 10 cm) filled with homogenized sand. Each plastic box contained 20 germinated seeds and was kept in darkness for 3 days; however, the plastic containers must be exposed to light for 3-4 hr every morning. All experiments were arranged in a completely randomized design (CRD) with three biological replicates, each replicate corresponding to a single container (20 seedlings).

Experiment 1

This study was conducted to determine the survival rate of six rice cultivars at submersion durations of 5, 10 and 15 days, following a protocol with modifications (12, 13). To simulate submergence during a high-turbidity flood, all the boxes were placed in darkness. After the submergence treatment, the water gradually drained from the containers. The number of seedlings that turned green after three days of exposure to natural light was used to calculate the survival rate. The percentage of surviving seedlings was calculated as the proportion that turned green and resumed growth.

Experiment 2

This experiment assessed the influence of light and darkness during submergence following a protocol with modifications (14). Seedlings were submerged either under light conditions (greenhouse; ~12 hr photoperiod) or complete darkness. Water was drained progressively from the boxes after the submersion procedure. The plastic containers were exposed to natural light for three days, and the percentage of seedlings that survived was determined by counting those that turned green.

Experiment 3

To examine the impacts of NO_3^- compounds on rice growth, rice seedlings were treated with 3 mg L^{-1} $Ca(NO_3)_2$, $Mg(NO_3)_2$, and $AgNO_3$ solutions. Rice seedlings (six-day-old) were submerged to a depth of 20 cm in solutions containing 3 mg L^{-1} $Ca(NO_3)_2$, $Mg(NO_3)_2$, or $AgNO_3$. The selected concentration was based on preliminary trials and published studies indicating that low-level NO_3^- application enhances hypoxia tolerance without causing ion toxicity (6, 8). In each box, 20 rice seedlings were flooded to a depth of 20 cm with different NO_3^- solutions. The solutions were poured out after various days of treatment. The percentage of seedlings that turned green was calculated after a 3-day recovery period.

Oxygen concentration measurement

To investigate the role of NO_3^- as a potential alternative electron acceptor, dissolved oxygen was measured daily between 10:00 and 12:00 AM using a dual temperature and O_2/pH meter (Oxi 330, WTW, Germany).

Soluble sugar content

Total soluble sugar concentrations were measured following a standardized protocol with modifications (15). Dried seedlings (0.5 g) were homogenized in 5 mL of 80 % methanol and incubated at 80 °C for 1 hr. After cooling on ice, supernatants (2 mL) were mixed with 0.5 mL of 5 % phenol and 2.5 mL of concentrated sulfuric acid (H_2SO_4) (98 %). The mixture was incubated at room temperature for 20 min, and absorbance was recorded at 490 nm. Glucose was used to construct the standard curve.

Statistical analysis

All experiments followed a completely randomized design (CRD) with three biological replicates per treatment. Data was analyzed using SPSS version 21.0. Normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) were verified before conducting one-way analysis of variance (ANOVA). When significant differences were detected ($p < 0.05$), means were compared using the least significant difference (LSD) test. Data are presented as mean ± standard deviation (SD).

Results

Effects of flooding on rice survival

As shown in Fig. 1A, apparent varietal differences were observed across the three flooding durations. After 5 days of submergence, IR64Sub1, OM7347, and OM4900 formed a statistically higher survival group ($p < 0.05$), while OM4218 and OM6976 clustered in the lower-survival group. Prolonged submergence (10 and 15 days) substantially reduced survival across all cultivars, with only OM7347 retaining >10 % survival at 15 days. Soluble sugar concentrations declined progressively with increasing submergence duration, with the lowest levels detected after 15 days (Fig. 1B). These findings indicate that flooding stress has induced adverse effects on modern rice survival in a time-dependent manner.

Effect of light and dark conditions on flooding stress

Light availability strongly influenced seedling survival (Fig. 2A). All cultivars displayed significantly higher survival under submerged light conditions compared with darkness ($p < 0.01$). In darkness, seedlings accumulated markedly higher soluble sugar concentrations (Fig. 2B), with increases ranging from 142-252 % relative to light-grown submerged seedlings. These findings indicated that light intensity and non-structural carbohydrate are essential for rice survival under flooding stress.

Effects of nitrate compounds on the growth of rice cultivars under flooding conditions

Nitrate supplementation influenced survival differently depending on compound and cultivar (Fig. 3A). Calcium nitrate significantly improved survival in OM4218, OM4900, and IR64Sub1 ($p < 0.01$), whereas $Mg(NO_3)_2$ and $AgNO_3$ showed limited effects except in OM4218. Shoot elongation responses differed among treatments: $AgNO_3$ stimulated significant elongation in all three cultivars ($p < 0.01$; Fig. 3B), while $Ca(NO_3)_2$ and $Mg(NO_3)_2$ produced minimal effects. Root length did not differ significantly among treatments (Fig. 3C). Calcium nitrate increased soluble sugar contents across cultivars ($p < 0.01$), and $AgNO_3$ enhanced sugar content in OM4218 ($p < 0.05$; Fig. 3D).

Variations of oxygen concentration

As shown in Fig. 4, dissolved oxygen concentrations initially increased during early submergence and subsequently declined with prolonged flooding. Under $AgNO_3$ treatment, the oxygen concentration at 1, 2, 4, 9, and 10 days for OM4900, OM4218, and IR64Sub1 was significantly higher than that of the other chemicals. Another NO_3^- treatment, $Ca(NO_3)_2$, gradually decreased oxy levels; however, their survival rate was usually higher than that of other treatments. When Ca present, these activities are delayed by 6, 7, or even 8 days after flooding. Therefore, the rice seedlings remained erect, healthy, and alive.

Discussion

Under abiotic stress, plants experience deficiencies in vital components and nutrient imbalances, leading to reduced yield and quality (16). Our time-course submergence assay showed that IR64Sub1, OM7347 and OM4900 maintained relatively higher

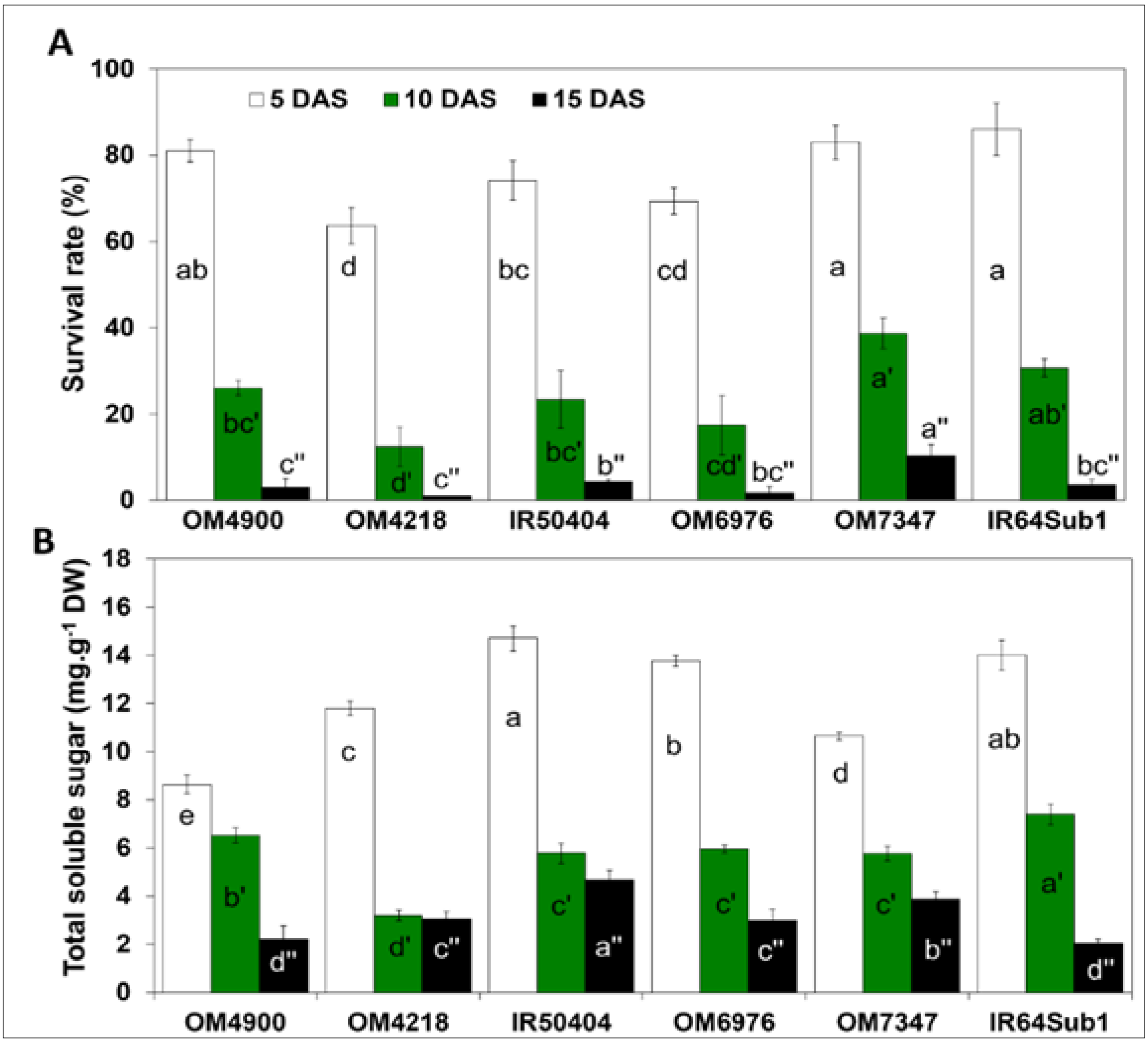

Fig. 1. Effects of submergence treatment on the (**A**): survival rate ± SD; (**B**) total soluble sugar content ± SD of six common rice cultivars. **DAS**: days after submergence. Data represents means of three independent replicates (n = 60 rice seedlings). Different letters indicate significant differences at $p < 0.05$, based on the LSD test.

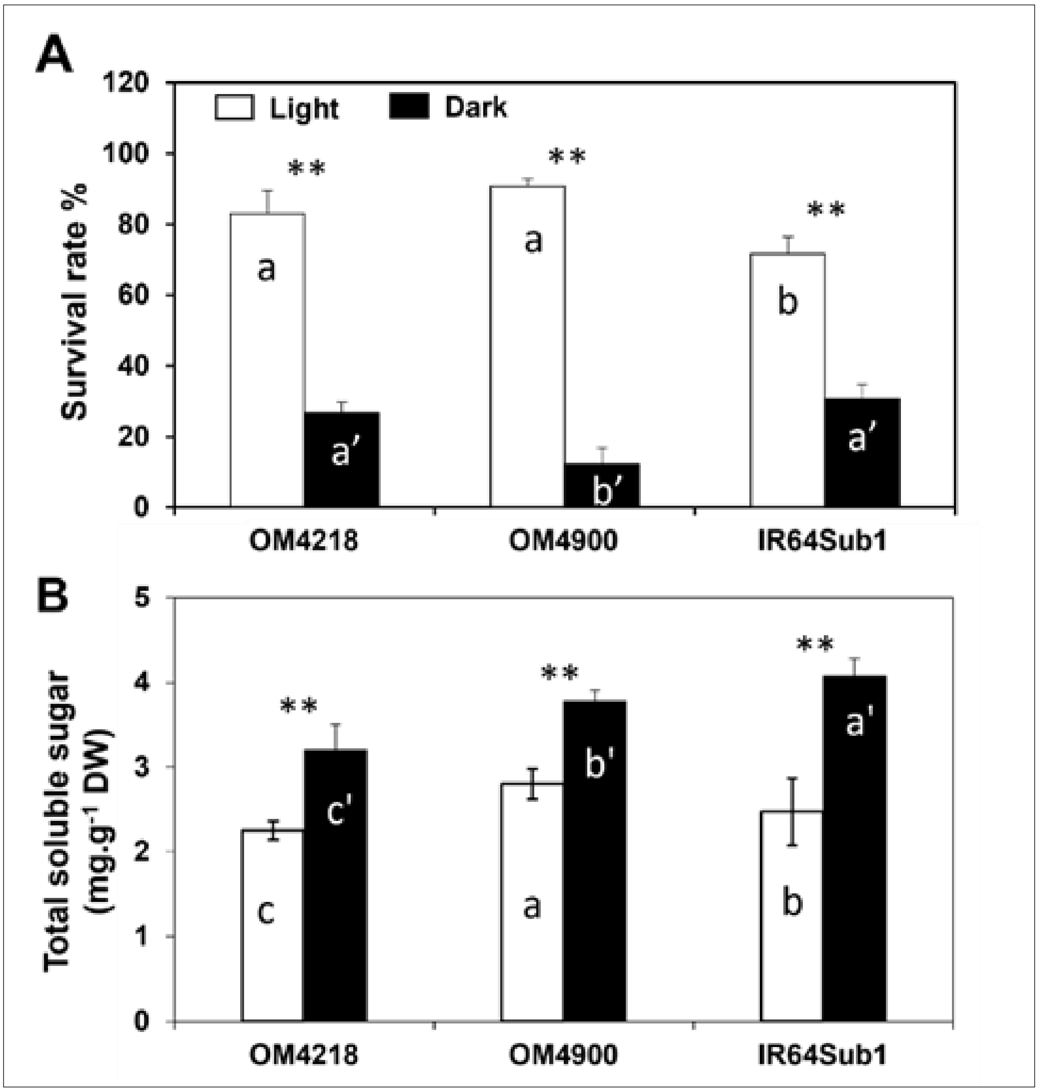

Fig. 2. Effects of light and dark conditions on the (**A**): survival rate ± SD; (**B**) total soluble sugar content ± SD in IR64Sub1, OM4900, and OM4218 cultivars after ten days of treatment. Data represents the mean of three independent replicates (n = 60 rice seedlings). Different letters indicate significant differences at $p < 0.05$, as determined by the LSD test.

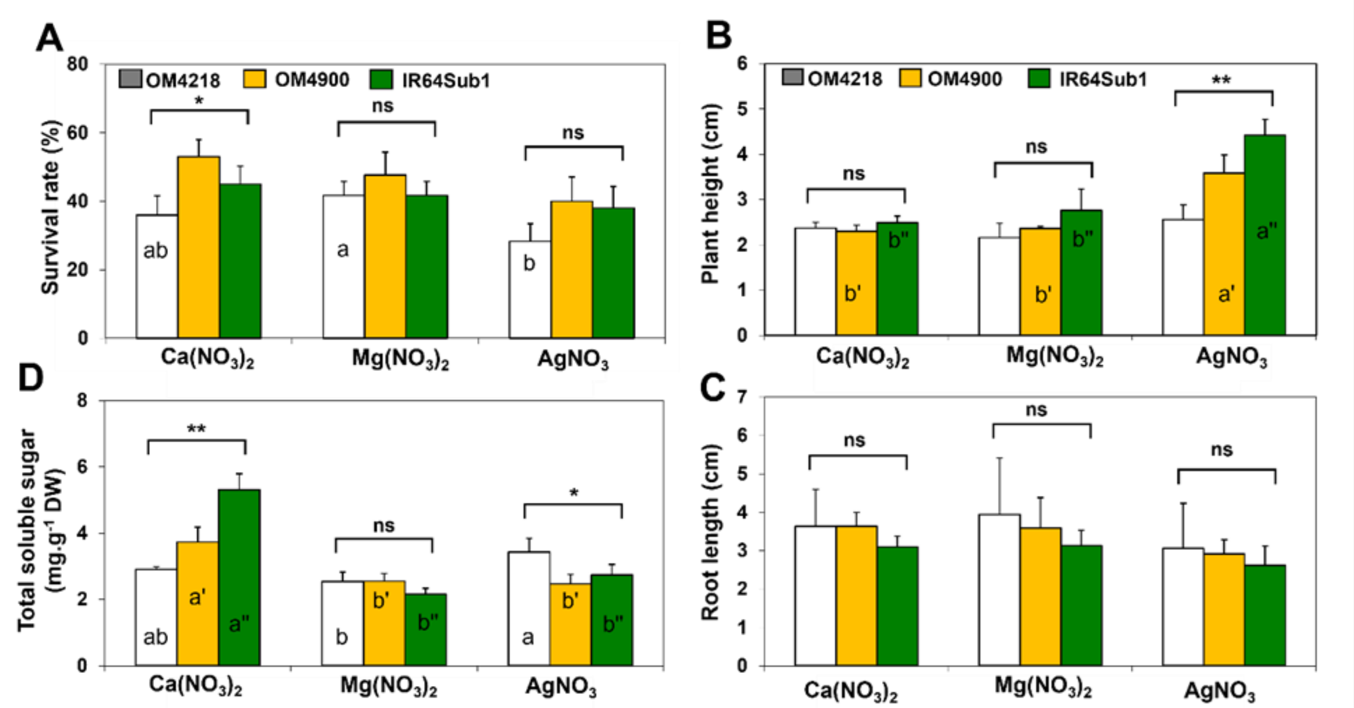

Fig. 3. Effects of $Ca(NO_3)_2$, $Mg(NO_3)_2$ and $AgNO_3$ on (**A**): survival rate ± SD; (**B**): plant height ± SD; (**C**): root length ± SD; (**D**): total soluble sugar ± SD in IR64Sub1, OM4900, and OM4218 cultivars after ten days of submergence treatment. Data represents means of three independent replicates (n = 60 rice seedlings). Different letters indicate significant differences at $p < 0.05$, based on the LSD test.

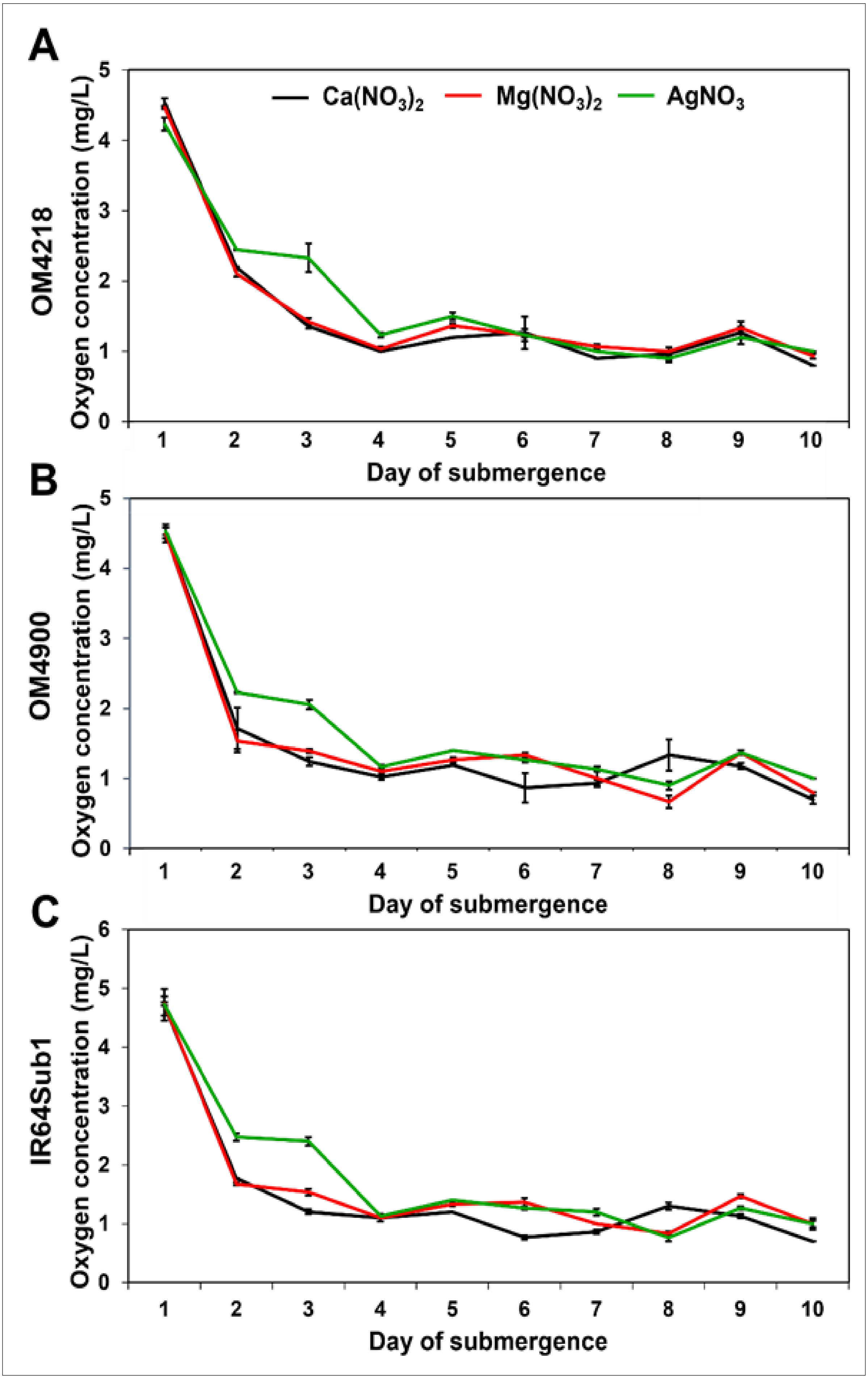

Fig. 4. Effects of $Ca(NO_3)_2$, $Mg(NO_3)_2$ and $AgNO_3$ on oxygen concentration ± SE in (**A**): IR64Sub1; (**B**): OM4900; (**C**): OM4218 cultivars after ten days of submergence treatment. Data represents the means of three plastic boxes - containing rice seedlings replicates (n = 3 boxes).

survival during short-term flooding, but survival dropped sharply beyond 10-15 days. This pattern is consistent with recent work on SUB1A-introgressed lines, where IR64Sub1 can tolerate about 7-14 days of complete submergence but still suffers substantial declines at longer durations (17). Most cultivated rice varieties can withstand about a week of flooding, whereas only a few landraces, such as FR13A, can survive prolonged submergence (2). Our data, therefore, placed OM7347, OM4900, and IR64Sub1 in a moderately tolerant group, but still below the extreme tolerance reported for FR13A and some recently improved lines (18).

The strong effect of light on survival in our study is consistent with the concept that underwater photosynthesis is crucial for sustaining carbohydrate supply during submergence. In one study, it was highlighted that tolerant genotypes typically conserve more non-structural carbohydrates and recover better after flood water recedes, whereas sensitive lines deplete their reserves faster (2). Similarly, several physiological studies report that higher soluble sugar and starch levels before and during submergence are positively associated with survival and recovery growth. Our finding that darkness led to much lower survival despite higher soluble sugar concentrations suggests that not only carbohydrate quantity, but also its efficient utilization under hypoxia, are key determinants of tolerance. This aligns with the idea that tolerant cultivars adopt a "quiescence strategy" to reduce energy consumption and avoid the wasteful use of carbohydrates during submergence (19).

The positive effect of $Ca(NO_3)_2$ on seedling survival connects well with emerging literature on the NO_3^- -NO_2^--NO pathway in low-oxygen tolerance. It was also proposed that NO_3^- reduction to nitrite and NO provides an alternative electron sink, helps regenerate NAD (P)- and buffers cytoplasmic acidosis during hypoxia (6). A study in cucumber showed that NO_3^- treatment alleviates waterlogging stress by enhancing NO-mediated anaerobic respiration, adventitious root formation, and NO_3^- transporter expression (8). We observed that $Ca(NO_3)_2$ increased both survival and soluble sugar content under complete submergence, which is consistent with these mechanisms. It suggests that NO_3^-, delivered as $Ca(NO_3)_2$, may support ATP production via NO_3^-–NO_2^- respiration and improve metabolic readiness for recovery in rice. Beyond the NO_3^- moiety, Ca also modulates flooding responses. Proteomic studies in soybean have shown that Ca supplementation under flooding enhances root elongation and suppresses cell death in the root tip (20). A proteomic analysis of soybean cotyledons under submergence suggested that Ca may participate in flooding-induced signal transduction via heat shock protein 70 (21). In another study, seed pelleting with calcium oxide (CaO) was found to enhance α-amylase activity while reducing alcohol dehydrogenase (ADH) and pyruvate decarboxylase (PDC) activities under waterlogging, thereby improving seed germination and seedling vigour in direct-seeded rice (22). Taken together, these findings support our interpretation that $Ca(NO_3)_2$ improves rice survival through a combination of NO_3^--fuelled anaerobic metabolism, Ca-dependent signalling, and structural protection.

In contrast, $AgNO_3$ had a distinct physiological profile: it promoted shoot elongation and maintained relatively high dissolved oxygen levels in the floodwater, but its effect on survival was weaker than that of $Ca(NO_3)_2$. Silver ions are classic inhibitors of ethylene perception, and several studies have used $AgNO_3$ to modulate flooding responses. Another study demonstrated that inhibition of ethylene signalling by $AgNO_3$ enhanced seed germination and submergence tolerance in rice (23). More broadly, ethylene is known to regulate both "escape" (rapid elongation) and "quiescence" strategies under low oxygen (24). Our finding that $AgNO_3$ enhances shoot growth under submergence is consistent with an ethylene-related shift in growth regulation; however, because ethylene inhibition does not directly enhance internal ATP production under hypoxia, $AgNO_3$ may primarily affect morphology and chlorophyll retention rather than the core energy crisis, which could explain why survival improvements are limited compared with $Ca(NO_3)_2$, despite higher oxygen levels in the water.

The higher dissolved oxygen observed under $AgNO_3$, but a stronger survival response under $Ca(NO_3)_2$, highlights an important point: external oxygen concentration is not the only determinant of submergence tolerance. Nitrate-driven internal electron-acceptor pathways and Ca mediated stress signalling may be more critical for sustaining metabolism than modest differences in water-column oxygen. This interpretation is supported by NO_3^- /NO studies in other species, which show that waterlogging tolerance is linked to restored root energy status and NO_3^- transport rather than to changes in bulk oxygen concentration.

Conclusion

Our observation indicated OM7347, IR64Sub1-the tolerant cultivars; OM4900, IR50404-, moderate cultivars and OM4218, OM6976- sensitive lines. Based on good correlations between light conditions and rice growth under complete submergence, it may be concluded that the reduction of rice survival in flooding results from reduced light intensity. Our work extends previous NO_3^- and Ca studies by demonstrating that low doses of $Ca(NO_3)_2$ and $AgNO_3$ can differentially modulate survival, growth and sugar status in rice seedlings under complete submergence. To fully resolve the mechanisms, future research should quantify NO_3^- reduction and NO production in rice tissues, examine the expression of NO_3^- transporters and hypoxia-responsive genes and dissect Ca- ethylene -NO crosstalk under flooding. Such mechanistic studies will be essential for translating our physiological findings into practical strategies to enhance rice resilience in flood-prone regions.

Acknowledgements

The authors are grateful to Cuu Long Delta Rice Research Institute for providing rice seeds.

Authors' contributions

PPN wrote the original draft, reviewed and edited the manuscript, provided resources, developed the methodology, conducted the investigation, curated the data and contributed to conceptualization, while NTDK wrote the original draft, reviewed and edited the manuscript, administered the project, developed the methodology, conducted the investigation, curated the data and contributed to conceptualization. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interest to declare.

Ethical issues: None

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