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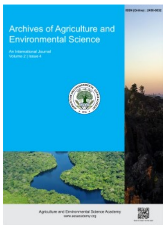

REVIEW ARTICLE

Impacts of submergence stress on rice plants and its adaptation: A review

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ABSTRACT

The main aim of this review is to convey information in summarized form by compiling and interpreting the major findings of recent studies on the impacts of submergence stress on rice and tolerance mechanisms. Published research papers available in Google Scholar, Web of Science, and Pub Med, mainly by Elsevier and SpringerLink, were critically analyzed and summarized for the preparation of the manuscript. In rice, plant survival rates, growth, and development are adversely affected by submergence. Major findings documented that submergence alters the soil aeration and creates hypoxic and anoxic conditions, which results in low photosynthetic efficiency and sugar status in rice plants. Compared to a tolerant cultivar, a sensitive cultivar produces more ethylene and causes injury to the plant. Controlled underwater shoot elongation, higher conserved non-structural carbohydrates, and better hormonal regulation, especially ethylene and gibberellin, and abscisic acid, are the primary adaptive mechanisms of tolerant plants in submergence, which helps better recovery at the post-submergence stage, too. The Sub1 gene and the associated QTLs are crucial for the superior performance of tolerant cultivars in submergence. Any agronomic management practices that can reduce ethylene production and enhance the nutrient status of plants can alleviate the severity of submergence. Understanding the intricate relationship between submergence and rice plant response is essential, mainly how submergence affects the rice plant and its tolerance mechanism to develop resilient rice cultivars that can grow in flood-prone regions.

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INTRODUCTION

Rice is the main food crop for almost half of the world's population (Banjade *et al.*, 2023). More importantly, South Asian countries consume ample amounts of rice in their daily kitchen. Rice can grow in a wide range of environments, but the recent climate alternation scenario has adversely lowered rice production and productivity (Khanal *et al.*, 2024). Rice cultivars generally tolerate a few days of complete submergence, but with duration, some cultivars also get acclimatized for prolonged submergence. Still, the seedling stage is more susceptible, and plants use adaptive and quiescence strategies to tolerate the submergence, where impact severity depends on the rice plants' age and the submergence duration (Ranawake *et al.*, 2014). Floods have detrimental effects on the internal aeration of paddy fields, the sugar status of rice plants, and survival (Winkel *et al.*, 2013), which is also mentioned in Figure 1. Irrespective of genotypes, the photosynthetic rate of completely submerged rice plants is lower than that of rice plants growing under control, partially submerged, and plants during the submergence recovery period, however it does not have a statistically significant correlation with growth parameters during submergence and post-submergence period (Sakagami *et al.*, 2013). The photosynthetic rate of rice plants growing under normal conditions is maintained consistently up to 21 days after flowering (DAF) however starts to deplete only after 7 DAF for submerged conditions, and the number of panicles, 1000 grain weight, spikelet number, and grain yield decreased by 12%,

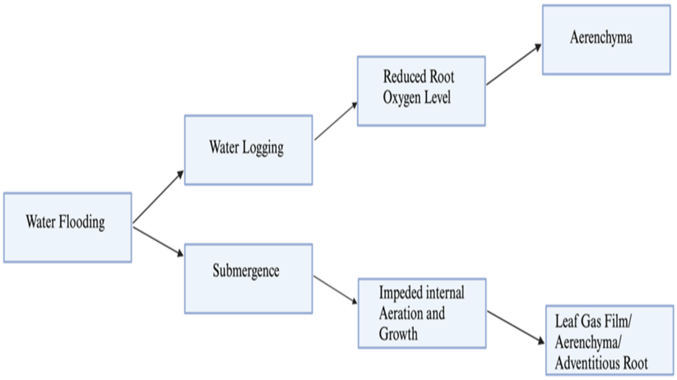

Figure 1. *Water flooding stresses, its impacts, and respective adaptations.*

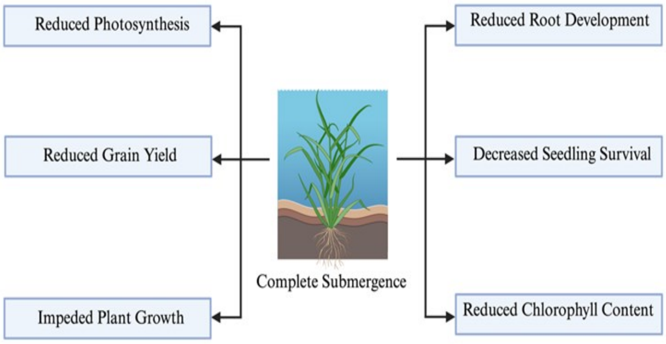

Figure 2. *Impacts associated with complete submergence on rice plant.*

19.3%, 13.3% and 13.7% respectively (Kumar *et al.*, 2011). The seedling survival of rice under water flooding is low where shoot length decreased by 81%, shoot greening delayed by 6-7 days, and root starts to appear only after 7-8 days of flooding (Ismail *et al.*, 2009). The percentage of survival of rice seedlings during submergence is positively correlated with the non-structural carbohydrates (NSC) after submergence and the extent of shoot elongation, where the rate of shoot elongation is positively correlated with NSC consumed during submergence but not correlated with NSC before submergence (Das *et al.*, 2005). In rice plants, the impacts of submergence can be lessened by minimizing the imbalance between energy production and its consumption, suppressing the ethylene-induced leaf senescence, and overexpressing the Sub1 locus in chromosome 9, which is influential on senescence, leaf elongation, and survival (Ahmed *et al.*, 2013). However, in the tolerant genotype, although there is low ethylene production at an early stage of germination, the ethylene production enhanced progressively after three days of flooding (Ismail *et al.*, 2009). Total above-ground dry matter content, chlorophyll content, and soluble carbohydrates significantly decreased in rice plants due to submergence stress, where some susceptible cultivars showed a 90% reduction in dry matter content (Sarkar & Bhattacharjee, 2011). At the post-submergence stage, the rice field reduces the leaf water potential and causes dehydration to the vegetative part of the rice plant, although the soil contains enough amount of water, which indicates that submergence is also associated with the sudden drought conditions of rice plants at the post-submergence stage (Fukao *et al.*, 2011).

METHODOLOGY

A comprehensive literature review was carried out for the manuscript preparation by using already available publications in Google Scholar, PubMed, Scopus, and Web of Science. The study was conducted by thoroughly reviewing, analyzing, evaluating, interpreting, and summarizing the main findings of different existing literature.

IMPACT OF SUBMERGENCE STRESS

Submergence stress significantly affects rice plant growth, plant biomass, panicle number, spikelet number, and harvest index, along with a delayed heading date and flowering day by seven days, leading to an 89% decrease in grain yield (Kato *et al.*, 2019). During submergence, growth parameters such as flowering date, plant height, tiller numbers, and chlorophyll content decrease, significantly impacting 14 days of submergence during the vegetative stage (Afrin *et al.*, 2018). Several research projects have reported that submergence and stagnant flooding stress significantly impact rice plants, as mentioned in Table 1. Sensitive cultivars exhibit a substantially reduced survival rate, while tolerant cultivars show higher survivability, attributed to increased root elongation and reduced shoot elongation (Bui *et al.*, 2019). The survival rate under submergence varies from 2.7% for susceptible cultivars to 82.9% for tolerant cultivars (Septiningsih *et al.*, 2012). Sensitive cultivars show reduced leaf, stem, and root dry weight, whereas tolerant ones maintain or slightly decrease these weights, correlating positively with survival after submergence (Singh *et al.*, 2014). Root tip activity is generally reduced, but tolerant cultivars maintain viability longer than sensitive ones (Bui *et al.*, 2019). Chlorophyll concentration decreases significantly for all genotypes under submergence, with sensitive cultivars experiencing severe damage, indicating faster leaf senescence (Bui *et al.*, 2019). Susceptible cultivars show a 10-20% greater reduction in chlorophyll than tolerant genotypes, associated with an 80-90% reduction in total soluble sugars and starch (Singh *et al.*, 2014). The significant impacts of complete submergence on the susceptible rice cultivars are mentioned in Figure 2. Additionally, complete submergence creates anoxic conditions, leading to sugar starvation in germinating seeds, potentially affecting sugar-dependent signaling pathways, sugar transporters, and downregulating oxygen-dependent genes (Lasanthi-Kudahettige *et al.*, 2007). The 14-20 days of flooding decrease growth rates at post-submergence by depleting non-structural carbohydrates by 74-77% (Sarkar & Bhattacharjee, 2011). Enzymatic activity is also affected; starch hydrolyzing invertase activity increases in submerged conditions, and AGPase and Rubisco enzyme activity decreases significantly (Kumar *et al.*, 2011). Lastly, water turbidity and silt deposition affect photosynthesis rates and survival due to stomatal clogging and shading effects (Gautam *et al.*, 2015).

Table 1. Major research findings from previous studies on crop responses to flooding treatment.

S. No.	Experiment	Flooding Treatment	Crop Response to Treatment	Conclusion
1	Increasing Flooding Tolerance in Rice: Combining Tolerance of Submergence and of Stagnant Flooding by (Kato *et al.*, 2019)	A water depth of 50 cm was maintained from 35 days after transplanting to maturity.	Yield Reduction by 48% for the dry season and 89% for the wet season.	The tolerance mechanism required for stagnant flooding differs from that of submergence stress.
2	Morpho-Physiological Changes in Roots of Rice Seedlings upon Submergence by (Bui *et al.*, 2019)	21-day-old seedlings were submerged for 12-14 days in a 1-meter-deep concrete tank.	Tolerant cultivars showed a higher survival rate and less shoot elongation but greater root elongation.	Root tip activity and root growth rate are significant factors associated with seedling survival after submergence.
3	Responses of Rice (*Oryza sativa* L.) Genotypes to Different Levels of Submergence by (Afrin *et al.*, 2018)	Rice plants were completely submerged for 7-14 days in the vegetative stage but only for seven days in the reproductive stage.	Total effective tillers per plant, above-ground dry weight, and rice grain yield were reduced.	Introgression of Sub 1 has its benefits to withstand submergence stress.
4	Physiological Basis of Tolerance to Complete Submergence in Rice Involves Genetic Factors in Addition to the SUB1 Gene by (Singh *et al.*, 2014)	For moderate stress, rice plants were completely submerged for 12 days, while for severe stress, only 17 days.	Root elongation, root, stem, and leaf weight, and chlorophyll content were higher but slower shoot elongation for tolerant cultivars.	FR13A-Sub 1A introgression is associated with better regulation of non-structural carbohydrates, which is crucial for seedling survival.
5	Submergence Tolerance of Some Modern Rice Cultivars at Seedling and Vegetative Stages by (Ranawake *et al.*, 2014)	Two weeks and six weeks old seedlings were completely submerged for seedling and vegetative stage study.	Only 24% of cultivars survived for 14 days of submergence, and cultivars with elongated shoots showed higher survivability.	The vegetative stage showed more severe damage for the same rice cultivar with the same submergence period than the seedling stage.

ADAPTATION MECHANISMS

Under stagnant flooding, culm physical strength increases by 25%, with a 24% reduction in bending stress and a 23% increase in culm diameter (Kato *et al.*, 2019). Tolerant cultivars maintain higher carbohydrate levels in roots at post-submergence, while all susceptible genotypes show reduced shoot carbohydrates (Bui *et al.*, 2019). During recovery, tolerant lines exhibit more tillers, faster leaf area recovery, and reduced lodging, aided by low underwater shoot growth and increased dry matter (Singh *et al.*, 2014; Kawano *et al.*, 2009). Ethylene accumulation in deepwater rice modulates gibberellin and abscisic acid interactions, promoting shoot elongation; tolerant cultivars accumulate less ethylene, conserving carbohydrates for shoot growth and cell division (Fukao & Bailey-Serres, 2008a). Tolerant genotypes display cell wall modifications and ethylene signaling, enhancing coleoptile development for oxygen uptake, with upregulation of genes related to cell wall modification (Hsu & Tung, 2017). Leaf gas films under submergence improve photosynthesis, sugar levels, and root aeration (Pedersen *et al.*, 2009). Sensitive cultivars have higher malondialdehyde and electrolyte leakage in roots, indicating more injury than higher peroxidase activity in tolerant cultivars (Bui *et al.*, 2019). Tolerant lines deplete starch faster and maintain soluble sugars during flooding, while intolerant lines deplete the starch at low rate (Lal *et al.*, 2018). Submergence reduces root elongation in rice, but tolerant genotypes maintain greater elongation, strongly linked to survival (Singh *et al.*, 2014). Flooding enhances Sub1A-1 activity, which disrupts gibberellin synthesis and reduces underwater shoot elongation. Increased tillering during submergence aids recovery, with reduced shoot elongation but enhanced dry weight in tolerant cultivars (Sakagami *et al.*, 2013). Finally, under hypoxic flooding conditions, tolerant genotypes convert more starch to soluble sugars, mobilizing them to develop shoots (Ismail *et al.*, 2009).

MANAGEMENT PRACTICES

The use of 1-methylcyclopropane to inhibit ethylene production conserves chlorophyll content, decreases chlorophyllase gene expression, reduces stem soluble sugar content, and ultimately enhances survival by 82% without significantly affecting underwater shoot elongation (Ella *et al.*, 2003). In flooded conditions, higher plant populations are achieved through the broadcasting method of seed sowing, but the highest yield is with drum seeding. Applying 20% more phosphorus along with recommended N:P:K ratios and higher seed rates increases plant height, tillering (64%), leaf area index, dry matter accumulation (17%), panicle density, and grain yield (Lal *et al.*, 2018). During submergence, gibberellin application depletes non-structural carbohydrates and reduces survival by 160-181%, whereas paclobutrazol conserves these carbohydrates, enhancing survivability by 44-55% (Das *et al.*, 2005). Applying nitrogen to rice seedlings before submergence is not recommended as it decreases chlorophyll concentration, reduces photosynthetic gas exchange by 25%, significantly alters the root-shoot ratio, and enhances shoot elongation during submergence, negatively affecting seedling survivability (Ella & Ismail, 2006).

GENETIC FACTORS BEHIND TOLERANCE

The Sub1 gene enhances the tolerance of rice cultivars to submergence stress at any growth stage from early seedling to the week before flowering. It provides the same agronomic and quality traits but with an enhanced yield of 1-3 tons/ha (Ismail *et al.*, 2013). The overexpression of Sub1A-1 confers tolerance to submergence, and the introgression of FR13A Sub1A-1 into different rice cultivars showed increased survivability to submergence with maintained grain yield (Xu *et al.*, 2006). In contrast, Sub1C does not confer tolerance to submergence, and the

Sub1C-1 allele is independent of the Sub1A-1 allele, however it can turn off the expression of the Sub1A-2 allele in combination and make rice plants intolerant to submergence (Septiningsih *et al.*, 2009). The introgression of Sub1 into rice cultivars increased the yield by 123-214%, enhanced the above-ground dry matter by 83-160%, increased the harvest index by 28%, increased the number of panicles per square meter by 38%, and filled grain percentage by 50% (Singh *et al.*, 2009). Rice genotypes tolerant to submergence conditions possess the Sub1 haplotype. In contrast, genotypes without Sub1 genes are susceptible to flooding, and some rice genotypes with only one allele of the Sub1 gene are moderately tolerant to flooding (Singh *et al.*, 2010).

The QTL region with the most significant effect on submergence tolerance is in chromosome 1, and its overexpression confers tolerance for submergence conditions, and tolerant cultivars show the highest expression of Sub1A (Septiningsih *et al.*, 2012). For submergence tolerance, five QTL are detected on chromosomes 1, 3, 7, and 9, contributing to phenotypic variation ranging from 17.9% to 33.5% (Angaji *et al.*, 2010). Three QTLs identified in chromosomes 1, 3, and 12, along with two novel QTLs, qTIL2 and qTIL4, detected on chromosomes 2 and 4, control the total internodal length in deep water rice (Nagai *et al.*, 2012). QTLs associated with seedling survival, stimulation of shoot elongation, and leaf senescence are detected on chromosome 9 (Toojinda *et al.*, 2003). In submerged conditions, the genes encoding pyrophosphate-dependent phosphofructokinase, glyceraldehyde-3-phosphate dehydrogenase, and pyruvate pyrophosphate dikinase are significantly upregulated, and genes encoding phosphoenolpyruvate carboxylase, cytochrome P450, and catalase are downregulated in tolerant lines (Hsu & Tung, 2017). Alcohol dehydrogenase activity has a crucial role in sucrose metabolism in both the embryo and endosperm to produce glucose and fructose for the growth and long-term survival of rice seedlings by proliferating cell division and elongation of coleoptile in submerged conditions (Takahashi *et al.*, 2014). The expression of pyruvate decarboxylase and alcohol dehydrogenase is higher in the tolerant genotype, with higher amylase activity under submerged conditions (Ismail *et al.*, 2009). The gene encoding for trehalose phosphate phosphatase (OsTPP7) expressed at higher levels in the tolerant genotypes and not detected in the susceptible genotypes is responsible for anaerobic germination during early germination. Gene OS-ACS5 encodes for 1-aminocyclopropane 1-carboxylic acid synthase responsible for ethylene production during submergence, which is responsible for the rapid elongation of shoot in deepwater rice (Van Der Straeten *et al.*, 2001). Rice plants accumulate more ethylene under flooding, which triggers the expression of SNORKEL1 and SNORKEL2 genes, encoding the ethylene response factor and causing internode elongation (Hattori *et al.*, 2009). The elongating coleoptile of the rice seed under submergence shows the expression of expansin genes, particularly EXPA7 and EXPB12, along with the involvement of ethylene response factors and heat shock proteins, which are highly crucial for the tolerance to flooding (Lasanthi-Kudahettige *et al.*, 2007). In tolerant genotypes, during submergence, the Sub1A gene promotes the accumulation of gibberellin (G.A.) signaling repressor Slender Rice-1 (SLR-1) and SLR-1 Like-1 (SLRL-1) in the aerial tissue of the rice plant, which regulates the shoot elongation and conserves the reserve carbohydrate for the post-submergence stage (Fukao & Bailey-Serres, 2008b). The detailed mechanism of ethylene-regulated expression of genes associated with shoot elongation in susceptible cultivars and Sub1A expression mediated reduced underwater shoot elongation in tolerant cultivars is mentioned in Figure 3.

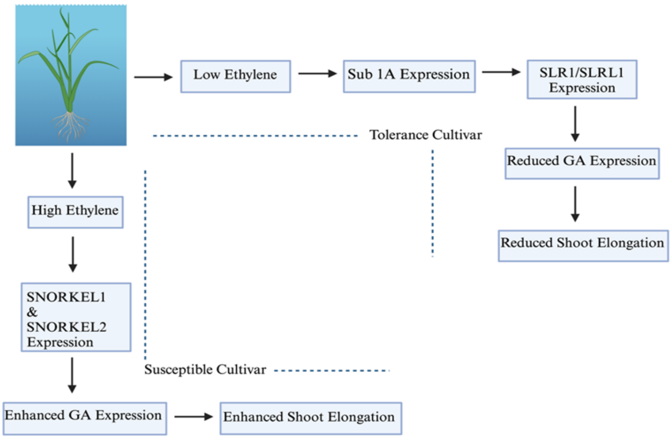

Figure 3. *Ethylene-dependent gene expression and its regulation to underwater shoot elongation.*

Conclusion

In conclusion, submergence stress negatively affects the various developmental and physiological traits and threatens the survivability of rice plants. However, tolerant cultivars show various adaptive mechanisms related to higher conserved carbohydrate content, low ethylene production, and regulated underwater shoot elongation. The presence of the Sub1 gene significantly enhances the survival rates and confers resiliency to waterlogging conditions. Introgression of the Sub1 gene into susceptible cultivars can also enhance rice plants' performance by increasing survival rate and photosynthesis efficiency in submerged conditions. Understanding the cellular, biochemical, and molecular basis of tolerance to submergence and integration of adaptive agronomic management practices is essential to lessen the harsh impacts of submergence. Further exploration of the genetic and molecular basis of tolerance and incorporation of modern, efficient breeding strategies should be the core of future research to develop cultivars that can grow happily in flooded areas and can support the goal of global food security in the scenario of climate change.

DECLARATIONS

Author contribution statement

Conceptualization, Methodology, Software and validation, Formal analysis and investigation, writing-original draft preparation: D. K.; Resources, Writing-review and editing, Visualization: D. K., B. B. and D. B. All authors have read and agreed to the published version of the manuscript.

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Ethics approval: This study did not involve any animal or human participant and thus ethical approval was not applicable.

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REFERENCES

Afrin, W., Nafis, M. H., Hossain, M. A., Islam, M. M., & Hossain, M. A. (2018). Responses of rice (Oryza sativa L.) genotypes to different levels of submergence. *Comptes Rendus - Biologies*, *341*(2), 85–96. https://doi.org/10.1016/j.crvi.2018.01.001

Ahmed, F., Rafii, M. Y., Ismail, M. R., Juraimi, A. S., Rahim, H. A., Asfaliza, R., & Latif, M. A. (2013). Waterlogging tolerance of crops: Breeding, mechanism of tolerance, molecular approaches, and future prospects. *BioMed Research International*, *2013*, 1-10. https://doi.org/10.1155/2013/963525

Angaji, S. A., Septiningsih, E. M., Mackill, D. J., & Ismail, A. M. (2010). QTLs associated with tolerance of flooding during germination in rice (*Oryza sativa* L.). *Euphytica*, *172*(2), 159–168. https://doi.org/10.1007/s10681-009-0014-5

Banjade, D., Khanal, D., Shrestha, A., & Shrestha, K. (2023). Effects of Seedling and Plant Spacing on the System of Rice Intensification (SRI) for Spring Rice (*Oryza sativa* L. Chaite 2). *AgroEnvironmental Sustainability*, *1*(3), 229–235. https://doi.org/10.59983/s2023010304

Bui, L. T., Ella, E. S., Dionisio-Sese, M. L., & Ismail, A. M. (2019). Morpho-Physiological Changes in Roots of Rice Seedling upon Submergence. *Rice Science*, *26*(3), 167–177. https://doi.org/10.1016/j.rsci.2019.04.003

Das, K. K., Sarkar, R. K., & Ismail, A. M. (2005). Elongation ability and non-structural carbohydrate levels in relation to submergence tolerance in rice. *Plant Science*, *168*(1), 131–136. https://doi.org/10.1016/j.plantsci.2004.07.023

Ella, E. S., & Ismail, A. M. (2006). Seedling nutrient states before submergence affects survival after submergence in rice. *Crop Science*, *46*(4), 1673–1681. https://doi.org/10.2135/cropsci2005.08-0280

Ella, E. S., Kawano, N., Yamauchi, Y., Tanaka, K., & Ismail, A. M. (2003). Blocking ethylene perception enhances flooding tolerance in rice seedlings. *Functional Plant Biology*, *30*(7), 813–819. https://doi.org/10.1071/FP03049

Fukao, T., & Bailey-Serres, J. (2008a). Ethylene-A key regulator of submergence responses in rice. *Plant Science*, *175*(1–2), 43–51. https://doi.org/10.1016/j.plantsci.2007.12.002

Fukao, T., & Bailey-Serres, J. (2008b). Submergence tolerance conferred by Sub1A is mediated by SLR1 and SLRL1 restriction of gibberellin responses in rice. *PNAS*, *105*(43), 16814-16819. https://doi.org/10.1073/pnas.0807821105

Fukao, T., Yeung, E., & Bailey-Serres, J. (2011). The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. *Plant Cell*, *23*(1), 412–427. https://doi.org/10.1105/tpc.110.080325

Gautam, P., Lal, B., Raja, R., Baig, M. J., Mohanty, S., Tripathi, R., Shahid, M., Bhattacharyya, P., & Nayak, A. K. (2015). Effect of nutrient application and water turbidity on submergence tolerance of rice (*Oryza sativa*). *Annals of Applied Biology*, *166*(1), 90–104. https://doi.org/10.1111/aab.12161

Hattori, Y., Nagai, K., Furukawa, S., Song, X. J., Kawano, R., Sakakibara, H., Wu, J., Matsumoto, T., Yoshimura, A., Kitano, H., Matsuoka, M., Mori, H., & Ashikari, M. (2009). The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. *Nature*, *460*(7258), 1026–1030. https://doi.org/10.1038/nature08258

Hsu, S. K., & Tung, C. W. (2017). RNA-Seq analysis of diverse rice genotypes to identify the genes controlling coleoptile growth during submerged germination. *Frontiers in Plant Science*, *8*, 762. https://doi.org/10.3389/fpls.2017.00762

Ismail, A. M., Ella, E. S., Vergara, G. V., & Mackill, D. J. (2009). Mechanisms associated with tolerance to flooding during germination and early seedling growth in rice (Oryza sativa). *Annals of Botany*, *103*(2), 197–209. https://doi.org/10.1093/aob/mcn211

Kato, Y., Collard, B. C. Y., Septiningsih, E. M., & Ismail, A. M. (2019). Increasing flooding tolerance in rice: Combining tolerance of submergence and of stagnant flooding. *Annals of Botany*, *124*(7), 1199–1209. https://doi.org/10.1093/aob/mcz118

Kawano, N., Ito, O., & Sakagami, J. I. (2009). Morphological and physiological responses of rice seedlings to complete submergence (flash flooding). *Annals of Botany*, *103*(2), 161–169. https://doi.org/10.1093/aob/mcn171

Khanal, D., Bastakoti, B., & Banjade, D. (2024). A Review: Elevated Nighttime Temperature Impacts on Rice. *International Journal of Plant & Soil Science*, *36* (8), 437–446. https://doi.org/10.9734/ijpss/2024/v36i84873

Kumar, A.D.A.K., M., Ghosh, N., Kumar Das Gupta, D., & Gupta, S. (2011). Impeded Carbohydrate Metabolism in Rice Plants under Submergence Stress. *Rice Science*, *18*(2), 116-126. https://doi.org/10.1016/S1672-6308(11)60017-6

Lal, B., Gautam, P., Nayak, A. K., Raja, R., Shahid, M., Tripathi, R., Singh, S., Septiningsih, E. M., & Ismail, A. M. (2018). Agronomic manipulations can enhance the productivity of anaerobic tolerant rice sown in flooded soils in rainfed areas. *Field Crops Research*, *220*, 105–116. https://doi.org/10.1016/j.fcr.2016.08.026

Lasanthi-Kudahettige, R., Magneschi, L., Loreti, E., Gonzali, S., Licausi, F., Novi, G., Beretta, O., Vitulli, F., Alpi, A., & Perata, P. (2007). Transcript profiling of the anoxic rice coleoptile. *Plant Physiology*, *144*(1), 218–231. https://doi.org/10.1104/pp.106.093997

Nagai, K., Kuroha, T., Ayano, M., Kurokawa, Y., Angeles-Shim, R. B., Shim, J. H., Yasui, H., Yoshimura, A., & Ashikari, M. (2012). Two novel QTLs regulate internode elongation in deepwater rice during the early vegetative stage. *Breeding Science*, *62*(2), 178–185. https://doi.org/10.1270/jsbbs.62.178

Pedersen, O., Rich, S. M., & Colmer, T. D. (2009). Surviving floods: Leaf gas films improve O 2 and CO 2 exchange, root aeration, and growth of completely submerged rice. *Plant Journal*, *58*(1), 147–156. https://doi.org/10.1111/j.1365-313X.2008.03769.x

Ranawake, A. L., Amarasinghe, G. S., & Senanayake, J. N. (2014). Submergence tolerance of some modern rice cultivars at seedling and vegetative stages. *Journal of Crop and Weed*, 10(2), 240-247.

Sakagami, J. I., Joho, Y., & Sone, C. (2013). Complete submergence escape with shoot elongation ability by underwater photosynthesis in African rice, Oryza glaberrima Steud. *Field Crops Research*, *152*, 17–26. https://doi.org/10.1016/j.fcr.2012.12.015

Sarkar, R. K., & Bhattacharjee, B. (2011). Rice Genotypes with SUB1 QTL Differ in Submergence Tolerance, Elongation Ability during Submergence and Regeneration Growth at Re-emergence. *Rice*, *5*(1), 7. https://doi.org/10.1007/s12284-011-9065-z

Septiningsih, E. M., Pamplona, A. M., Sanchez, D. L., Neeraja, C. N., Vergara, G. V., Heuer, S., Ismail, A. M., & Mackill, D. J. (2009). Development of submergence-tolerant rice cultivars: The Sub1 locus and beyond. *Annals of Botany*, *103*(2), 151–160. https://doi.org/10.1093/aob/mcn206

Septiningsih, E. M., Sanchez, D. L., Singh, N., Sendon, P. M. D., Pamplona, A. M., Heuer, S., & Mackill, D. J. (2012). Identifying novel QTLs for submergence tolerance in rice cultivars IR72 and Madabaru. *Theoretical and Applied Genetics*, *124*(5), 867–874. https://doi.org/10.1007/s00122-011-1751-0

Singh, N., Dang, T. T. M., Vergara, G. V., Pandey, D. M., Sanchez, D., Neeraja, C. N., Septiningsih, E. M., Mendioro, M., Tecson-Mendoza, E. M., Ismail, A. M., Mackill, D. J., & Heuer, S. (2010). Molecular marker survey and expression analyses of the rice submergence-tolerance gene SUB1A. *Theoretical and Applied Genetics*, *121*(8), 1441–1453. https://doi.org/10.1007/s00122-010-1400-z

Singh, S., Mackill, D. J., & Ismail, A. M. (2009). Responses of SUB1 rice introgression lines to submergence in the field: Yield and grain quality. *Field Crops Research*, *113*(1), 12–23. https://doi.org/10.1016/j.fcr.2009.04.003

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*, *6*. https://doi.org/10.1093/aobpla/plu060

Toojinda, T., Siangliw, M., Tragoonrung, S., & Vanavichit, A. (2003). Molecular genetics of submergence tolerance in rice: QTL analysis of key traits. *Annals of Botany*, *91*(2), 243–253. https://doi.org/10.1093/aob/mcf072

Van Der Straeten, D., Zhou, Z., Prinsen, E., Onckelen, H. A. Van, & Van Montagu, M. C. (2001). A Comparative Molecular-Physiological Study of Submergence Response in Lowland and Deepwater Rice. *Plant Physiology*, *125*(2), 955-968. https://doi.org/10.1104/pp.125.2.955

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 O2. *New Phytologist*, *197*(4), 1193–1203. 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*(7103), 705–708. https://doi.org/10.1038/nature04920