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Assessing the Impact of Elevated Temperature and Water Limitation on Yield Production, and Seed Longevity of Aerobic Rice cv. MRIA 1

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ABSTRACT

This research was conducted at the Faculty of Plantation and Agrotechnology, Universiti Teknologi MARA (UiTM) from February to May 2021. The study objectives were to determine the effects of environmental factors, water limitation (WL) and high temperature (HT), on yield production and seed quality development of aerobic rice cv. MRIA 1. The seed was cultivated in a glass house (25/45°C min/max) and subjected to 3 days of WL and HT (25/40ºC 12 photoperiod) at different seed development stages [8, 14, 21, and 28 days after anthesis (DAA)] with four replications. Plants treated from 21 to 28 DAA showed tolerance to WL and HT, while the detrimental effect occurred at 8 DAA and 14 DAA. Normal germination (>90%) was obtained from the control, and the plant had reached physiological maturity at 21 and 28 DAA. As plant treated to environmental stress, the amylose concentration obtained ranges from 9 to 14%. The lowest seed longevity (p50) obtained from plants treated at 14 DAA recorded only 3 days, and the longest was from control seed obtained for 26 days. In conclusion, exposing cv. MRIA to HT and WL at late maturation stage has less effect on yield production and seed quality development.

INTRODUCTION

Rice is a staple food crop that is grown in many parts of the world. There are various methods of cultivating rice, depending on local conditions and technology, such as aerobic rice cultivation. Through this aerobic cultivation, it supports water saving, particularly in water-scarce area. The aerobic rice system is a water-efficient methods of planting rice in non-puddled soil that thrived in well-drained conditions. In contrast, the flooded rice system used the high-water usage and risk to the greenhouse gas emission. Liu et al. (2021) had proved that planting aerobic rice is able to reduce 30% of water usage and 70% of methane gas emission. Ishfaq et al. (2020) reported that the rice yield production increased up to 30%, therefore positioning it as a favorable option especially for small-scale farmers. However, Zaman et al. (2019) reported that the flooded-rice cultivar (MR253) produced a higher grain yield as compared to the aerobic rice cultivar (MRIA-1) under normal aerobic conditions but can still produce a reasonably high yield under water stress conditions. Alejo (2021) had suggested the cultivation of aerobic rice potential to promote sustainable practices in rice production, as aerobic rice adapted well to unfavorable condition resulting from global warming disruption. The first Malaysian aerobic rice, known as MRIA-1, was developed by the Malaysian Agricultural Research and Development Institute (MARDI) through the breeding program using rice lines from the International Rice Research Institute (IRRI) in 2005. Sariam et al. (2015) stated that the MRIA-1 aerobic rice was successful developed through chemical mutation of IR 76569-259-1 and has the potential to produce a grain yield of about 4-5 t/ha.

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Global temperature rose either from natural processes or human activities that released greenhouse gas emissions (GHGs). Flooding rice cultivation in field consumes large amounts of water resource and, therefore contributes to GHGs in the environment (Ishfaq et al., 2020). Similar to other countries, Malaysia is also facing the climate change incident such as rising in temperature which arise not only from its own GHGs but also from the global warming phenomenon (Keshmider, 2018). Globally, this phenomenon results from intensified change in rainfall patterns and drought conditions, which later might contribute to our food security system; therefore the awareness and mitigation efforts need to be a concern. Without effective mitigation strategies for climate change, global rice yield production is projected to decrease between 3% and 12% by mid-century and 11% and 25% at the end of the century. Drought condition is a major cause in the declining of rice production as reported by Cheng et al. (2025), whereas the rice crop is expected to lose up to 13% once, there is an increase of 2°C from climate warming scenario.

Meanwhile, according to Zhao et al. (2017), rice productivity is projected to decline by approximately 3.2% for every 1°C increase in temperature, resulting from rice seed quality degradation (Zandalinas et al., 2018). Rusli et al. (2022) reported that climate change poses a serious threat to rice production, which will in turn affect food security as they are highly correlated. Therefore, an adequate measurement of the use of water resources is needed for rice cultivation to manage the sustainable farming practices.

Climate change, caused by elevated temperatures, contributes to the seed production quality, such as seed size, filling rate duration, germination capacity, and deterioration rate. At the reproductive and grain-filling phases, rice plants can have detrimental effects on grain yield and quality as they are exposed to high temperature (HT) (Arshad et al., 2017; Oh et al., 2023). Verma & Kanwar (2020) stated that rice production is facing a threat to its sustainability as the frequency and intensity of HT. Generally, this factor was due to the spikelet sterility during the heading stage, which later affects the grain filling rate and rice yield production (Oh et al., 2023). During the panicle initiation stage, HT causes deterioration in the spikelet and then damages the development of the floral organ. However, the adaptation towards HT depends on the varieties, whereas Wang et al. (2019) had claimed that the Indica rice varieties demonstrate the highest tolerance to HT, followed by the Japonica rice varieties. Seed viability can be defined as the capability of seeds to produce healthy seedlings with normal germination, which is a main factor in order to produce successful crop production (Finch-Savage & Bassel, 2015; Reed et al., 2022). Environmental stresses such as HT and drought conditions significantly reduce seed viability and contribute to threat to rice productivity. Research indicates that both abiotic factors adversely affect seed quality development, therefore leading to poor emergence and stunted seedling growth. Even short periods of heat stress imposed particularly at the seed-filling stage, able to accelerate maturation, results in seed quality development, and reduce crop yield production (Abdul Rahman & Ellis, 2019).

Seed longevity can be defined as the capability of seeds to continue to be viable in storage. It is a crucial element in rice cultivation and breeding programs, as it determines the seed vigor over time. One of the factors that influence seed longevity are exposure to HT (Hay et al., 2022) and terminal drought (Abdul Rahman & Ellis, 2019) during rice cultivation, particularly during the seed-filling phase. Elevated temperature stress has a significant impact on the physiology and biochemistry of seeds and, leads to numerous detrimental effects, such as damaging proteins by disrupting their synthesis, inactivating essential enzymes, and causing loss of membrane cell integrity. Both cellular and molecular changes might limit plant growth and contribute to oxidative damage, therefore reducing seed longevity capability (Fahad et al., 2017). Various crop species, including soybeans and wheat, have observed the effects of high temperature on seed longevity. Researchers have shown that high-temperature stress during the seed-filling stage in rice (Abdul Rahman & Ellis, 2019) and soybeans reduces yields and alters seed compositions (Yang et al., 2023).

Climate changes have received less attention to rice seed quality than yield. As rice is a main food crop, making sure there are enough yields to meet national demand depends on the quality of the seeds. This study was conducted to examine the yields and seed quality as the environment was stressed (high temperature and water limitation) during the stage of seed development and maturation, specifically aerobic rice seed cv. MRIA 1.

MATERIALS AND METHODS

The study was carried out at the Faculty of Plantation and Agrotechnology, UiTM Jasin Melaka, Malaysia (2°13'39.1"N 102°27'27.2"E). The seed was sown on 11th February 2021, representing 0 days after sowing (DAS), and was harvested on 10th May 2021, which corresponds to 88 DAS or 34 days after anthesis (DAA). Initially, the aerobic seed (cv. MRIA 1) was obtained from the Malaysian Agricultural Research and Development Institute (MARDI) Seberang Perai, Pulau Pinang, Malaysia, and was multiplied at UiTM Jasin to serve as seed material. Prior to sowing, the seed viability of cv. MRIA 1 was tested and showed 99% germination. The soil of the Gajah Mati series was used as a planting medium, obtained from the UiTM Share Farm area. Soil was mixed with organic soil in a 2.5:1 ratio and was filled in the 14-liter pots.

Plant Husbandry

The rice plant was subjected to high temperature (HT) and water limitation (WT) treatments for three (3) days at different stages of seed development (8, 14, 21, and 28 DAA) and was laid out using Completely Randomized Design (CRD). Seven seeds were directly sown in each pot in the greenhouse (GH) condition. After 14 DAS, only five seedlings remained per pot. The rice plants were watered with 1.5 liters of water per pot twice per day. Fertilizer NPK Green (15:15:15) was applied as recommended by MARDI (2015). A pesticide application with Wesco Malathion 57 (Hextar Chemical Sdn. Bhd.) was manually sprayed directly on the plants at flowering stages [45-80 days after sowing (DAS)] to control pests during milking stages. The plants were transferred from the GH to the growth chamber (Percival Scientific) for HT treatment, set up at 28/40°C with a 12-hour photoperiod and 75±0.5% relative humidity. Water supply to the rice plants has been terminated for three (3) days and then continued until harvest maturity. The determination of the rice plant to achieve 50% anthesis has been recorded, represented as an indicator to identify the stages of seed development, which is purposely important for imposing environmental stress. In this study, plants had reached 50% anthesis at 55 DAS.

Data Collection

The plant biomass, seed fresh weight (SFW), and seed dry weight (SDW) of aerobic rice were collected at five (5) series of harvesting (7, 13, 20, 27, and 34 DAA) to identify the growth pattern of aerobic rice once subjected to HT or WL. The number of panicles per pot produced was counted, and freshly harvested seeds were weighed (g). Seed moisture content (MC) and 1000-seed dry weight (SDW) were determined on a fresh weight basis (ISTA, 2009). The plant biomass was determined by separately drying the shoot and root at 60°C for 48 hours. For seed quality parameters, the data were recorded at 34 DAA-harvest maturities. The ability of seed to germinate normally was tested in moist rolled paper in a growth chamber set up at 35/28°C with a 12-hours photoperiod for 14 days. The firmed seed remained after 21 days, extended until 28 days. Ten normal seedlings for each replicate were randomly assessed for the seedling length and dry matter at 14 DAS. The dry matter of the seedling was examined by weighing and drying it in a constant oven. The seed vigor index (SVI) has been calculated using the formulation of seedling length derived from seedling length and percentage of final normal germination. The percentage of amylose content cv. MRIA was determined according to Serna-Saldicar (2012) by using the corresponding absorbance for 2.5 ml of the test solution.

RESULTS AND DISCUSSION

Yield of cv. MRIA Affected by Environmental Stress

Fig. 1 illustrates the yield pattern (plant biomass, seed fresh weight (SFW), and seed dry weight (SDW)) of aerobic rice cv. MRIA during five harvesting cycles, while the plant is exposed to both WL and HT. Results for plant biomass showed there were no significant differences between the main treatment (HT/WL) and also between the main treatment and sub-treatment (different seed development). But exposure to HT and WL at the vegetative stage significantly reduced plant biomass; particularly at high temperatures (HT), plant biomass was significantly lower at 8 DAA (173.47 g) than the control (195.80 g). This contradicts the previous studies that suggest WL has a greater impact on plant biomass than HT. Vibhuti et al. (2015) reported that intense water stress led to a reduction in plant biomass by shortening the plant's growth period (Yang et al. (2017). Wassie et al. (2019) reported that HT alters the morphological process in the plant by inhibiting the growth of plant shoots. In addition, Fahad et al. (2017) have reported that severe water stress during the reproductive stage reduces the plant root dry weight and plant biomass, as this stress limits the supply of water and nutrients to the upper ground parts of the plant.

The result shown in Fig. 1, demonstrated that HT had a significant effect on SFW. The data for SFW for sub-treatments at 8 and 14 DAA were significantly lower than the control. But there was no significant difference between the control during 21 and 28 DAA. This finding, similar to Zaman et al. (2018), indicated that WL imposed at all selected growth stages significantly reduced the grain yield of lowland rice, but not aerobic rice. Drought during anthesis increases panicle temperature and leads to heat damage affecting spikelet fertility and grain set. Lawas et al. (2018) reported that soil water limitation decreased panicle number and increased panicle temperature up to 3.3–3.9℃ higher than ambient temperature, resulting in heat stress, particularly when water limitation occurred during anthesis and therefore decreased grain set and grains per panicle. Only at the panicle initiation stage does the water stress significantly reduce the grain yield of aerobic rice. Yield components also declined dramatically with water deficits, particularly during flowering, pod setting, and pod filling stages. According to Zaman et al. (2018), water stress during the late heading stage led to lower grain production than water stress exposed after 10–25 days later. Coast et al. (2020) reported that HT either before or during the anthesis process reduced the seed set in the rice plant. Heat stress during the reproductive and grain-filling stages led to significant grain yield losses due to decreased size and fertility of seeds (Begcy et al., 2018).

The present study showed that the SDW of cv. MRIA had a significant effect for both treatments, HT and WL, and the reduction of SDW was more pronounced in HT with 53.31 g than WL with 59.03 g. The WT treatment did not show significant differences in SDW per pot between the control and treatments. Environmental stress at an early stage of seed development (8 and 14 DAA) resulted in the lowest SDW (38.99 g; 50.66 g) and demonstrated a highly significant difference compared to the control (60.36 g). Similar to SFW, there was no significant interaction between treatment and stages of seed development. Significant variation exists among rice germplasms in response to temperature stress, indicating the need to understand the specific impact of heat stress during different developmental stages (Xing et al., 2024). Sandhu et al. (2021) have observed that transient DNA heat stress during early seed development in rice reduces seed size by altering endosperm development. Moreover, the response of phytohormone homeostasis to heat stress in rice plants varies during different developmental stages. This suggests that the specific stage at which heat stress occurs may influence its effects on seed development (Abdul Rahman & Ellis, 2019). Fig. 1 shows the pattern of yield production (plant biomass, seed fresh weight (SFW), and seed dry weight (SDW) of aerobic rice cv. MRIA at five series of harvesting as plants are exposed to WL and HT.

Seed Quality of cv. MRIA Affected by Environmental Stress

In Table 1, the result showed that 1000 SDW was significantly lower for HT (18.03 g) than WL (21.98 g) at 8 DAA. However, there were no significant differences between 1000 SDW of HT and WL treatment at 14, 21, and 28 DAA. The detrimental effects of water scarcity on rice development, panicles, spikelet counts, and grain filling, resulting in a decrease in the 1000-grain SDW (Hang et al., 2022). Abdul Rahman & Ellis (2019) found that water limitation during the early stage of seed development significantly lowered the 1000-grain weights of both Indica rice varieties, Gleva and aerobic rice cv. Aeron 1.

When exposed to HT or WL, the seed MC of cv. MRIA showed a significant difference at early seed development, reducing to 15.63% and 20.91% at 8 and 14 DAA. At the later stages of seed development, there was no significant difference between the control group (24.43%) and the MRIA group (24.42%) at 21 DAA and 23.05% at 28 DAA (Table 1). Water limitation not only decreases the seed moisture content and reduces the SDW, but it also accelerates seed development and the early completion of seed filling, as reported by Abdul Rahman & Ellis (2019). Water stress and elevated temperatures have a profound impact on the rice grain quality, therefore affecting the moisture content and subsequently influencing the growth, development, and yield production (Kide Mengistu, 2022). Thus, the proper water schedule and temperature control should be implemented during critical growth stages (seed development phase) in order to achieve desirable seed moisture content and later enhance seed quality and obtain optimal rice growth, development, and yield production. Debabrata et al. (2021) reported that water scarcity occurred during seed development, simultaneously posing seed moisture loss and therefore incurring poor germination ability.

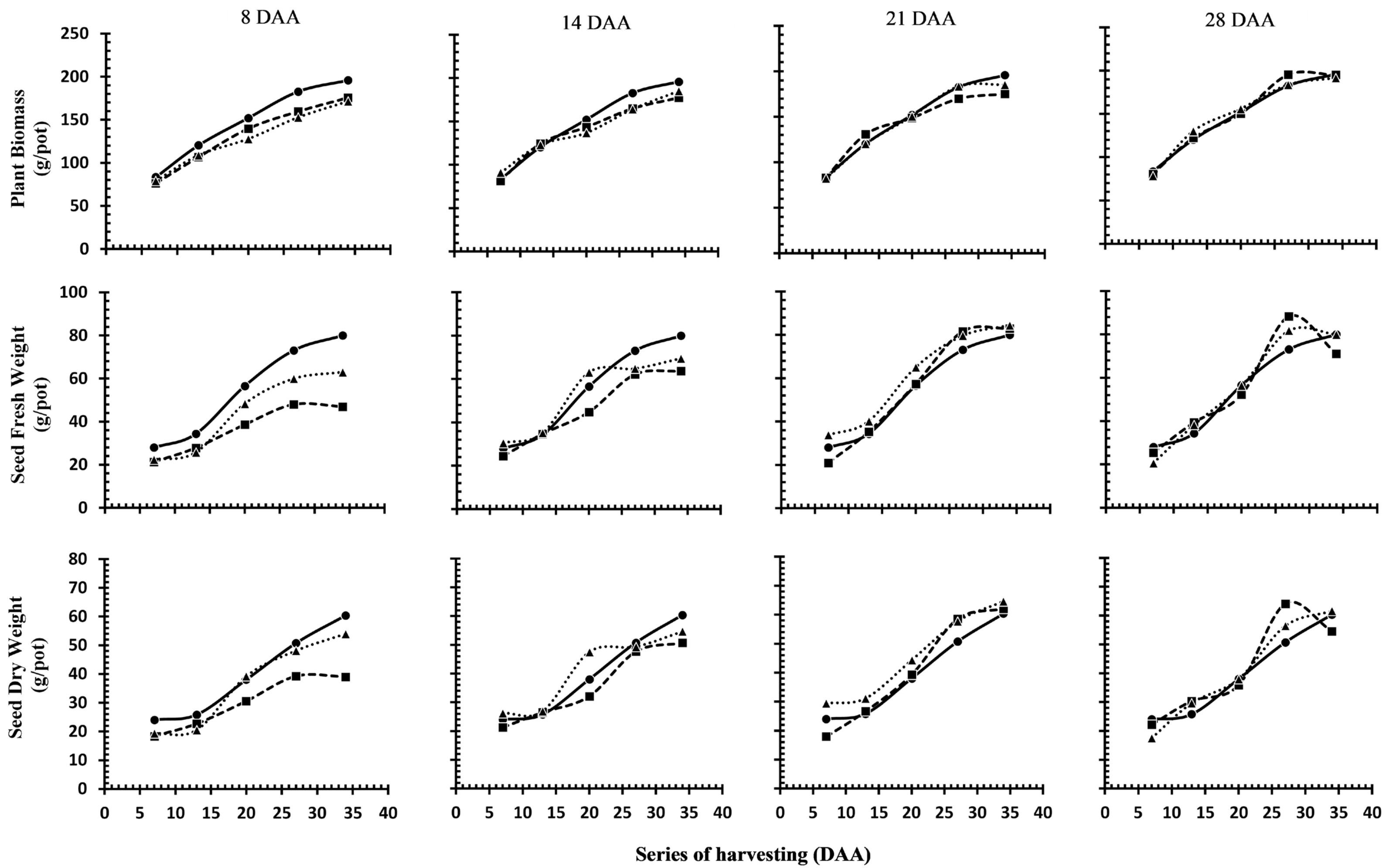


Fig. 1. Yield of cv. MRIA as exposed to HT at 28/40 °C with a 12-hour photoperiod and 75±0.5% RH (■) / WL with water limitation (▲) for 3 days during seed development (8, 14, 21, and 28 DAA) at five series of harvesting (7, 13, 20, 27, and 34 DAA). The control as the normal cultivation condition (●).

Table 1. Effect of 3-day WL and HT treatments at different seed development stages on seed quality of cv. MRIA at harvest maturity (34 DAA).

Treatment	Sub-treatment (DAA)	Seed quality of cv. MRIA							
		1000 seed dry weight	M.C (%)	Germination (%)	Speed germination	Energy of germination	Seedling length (cm)	Seedling biomass (g)	Seedling vigor index (SVI)
	Control (without stress)	24.38±0.77	24.43±0.90	98.66±1.15	0.98±0.01	18.66±2.51	23.86±0.81	0.154±0.021	2354.14±63.98
High temperature (40 °C)	T1 - 8	18.03±0.52	16.95±1.41	76.66±4.61	1.00±0.00	7.00±3.60	18.80±1.04	0.137±0.010	1440.57±87.83
	T2 - 14	20.10±0.25	20.42±0.98	88.00±2.00	0.99±0.01	17.66±1.52	18.10±2.62	0.145±0.009	1593.83±263.35
	T3 - 21	21.81±0.61	25.21±1.72	95.33±3.05	1.00±0.00	20.00±3.60	16.03±2.17	0.161±0.008	1530.75±252.67
	T4 - 28	21.87±0.25	23.28±0.07	96.00±0.00	1.00±0.00	17.66±2.08	17.30±1.49	0.149±0.005	1661.12±143.25
Water limitation	T1 - 8	21.98±0.25	14.32±1.01	84.66±2.30	1.00±0.00	11.00±1.73	21.06±1.88	0.158±0.014	1782.74±145.74
	T2 - 14	20.52±0.90	21.39±1.24	94.00±3.46	1.00±0.00	20.00±1.00	21.16±0.49	0.167±0.005	1991.76±119.46
	T3 - 21	21.10±0.36	23.43±1.57	96.66±2.30	1.00±0.00	18.66±1.52	19.76±0.80	0.150±0.004	1912.39±109.28
	T4 - 28	22.42±0.70	22.82±1.96	96.66±2.30	1.00±0.00	15.66±1.52	20.16±2.31	0.157±0.011	1944.48±203.47
Treatment		<.001	.064	.003	.570	.488	<.001	.063	<.001
Sub-factors		<.001	<.001	<.001	.006	<.001	<.001	.740	<.001
Treatment* sub-factors		<.001	.064	.047	.852	.175	.349	.120	.227

Remarks: *The values are expressed as means ± standard deviations

When cv. MRIA seeds were exposed to HT or WL early in their development, they grew much less successfully than the control (92.67%). As plants were exposed to 8 and 14 DAA, they produced seed that grew the least successfully, with only 68.00% and 76.33%, respectively (Table 1). The HT treatment significantly reduced seed germination compared to WL at 8 and 14 DAA. Khaeim et al. (2022) suggest that a temperature range of 20°C is ideal, with an optimal range of less than 30°C, particularly during the grain-filling stages. Some genes' DNA methylation status changes, which slows down or speeds up transcription levels during imbibition stress. This makes it take longer for rice seeds to germinate in some varieties when heat stress is present during grain filling (Suriyasak et al., 2021). Vibhuti et al. (2015) demonstrated that a decline in germination with increasing water stress, reducing from 68.8% to 4.4% at the highest stress level. However, contradicting Begcy et al. (2018) found that transient heat stress during early seed development increased the germination rate in rice seeds. This might happen right due to dormancy for some rice varieties.

Speed of Germination

The results indicated that the speed of germination was significantly higher in the control than in the plant treated with HT and WL at 8, 21, and 28 DAA, respectively. Liu et al. (2019) found that abscisic acid (ABA), reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and superoxide anion($O_2^{\cdot-}$), and malondialdehyde levels rose in seeds when they were exposed to HT and WL stress. This can stop rice seeds from germinating and seedlings from establishing. Huang et al. (2020) found similarly that drying rice seeds at high temperatures causes a lot of reactive oxygen species (ROS) to build up and make antioxidant enzymes work better in the seeds. Chao et al. (2021) found that genotypic differences and barriers to water absorption in the hull and pericarp can influence germination speed.

Germination Energy

According to Bam et al. (2006), the term germination energy refers to the proportion of germinated seeds after 72 hours, whereas it provides a quick and reliable measure of seed viability and seed vigor. The present study has shown that the treatment of HT or WL showed no significant difference in the energy of germination for cv. MRIA. The results prove that HT and WL during early seed development (8 DAA) reduce the energy of germination in seed rice (Table 1). Exposed HT and WL during seed development play a crucial role in affecting the energy of rice seeds. Many studies had proved that water stress, particularly drought, inhibits metabolic activation in the germination process and cause stunted rice plant growth. Silva et al. (2022) indicated that water limitation reduces the speed and energy of imbibition in rice seed, which is important to induce the initial metabolism during germination. In the present study, both HT and WL stresses significantly influenced various physiological processes in rice seeds, including the rice seeds' energy, seed longevity, ability to produce normal germinants, and yield production.

Length of Seedling

From this study, it indicates that the HT treatment had a greater impact on the length of the seedlings of cv. MRIA as compared to the WL treatment (Table 1). Vibhuti et al. (2015) and Hussain et. al. (2018), both studies had proved a consistent finding with the present study, reporting that seeds that had been exposed to water stress had a significant reduction in seedling length. The growth and vigor of seedlings are sensitive to temperature, with extremely high temperatures leading to a reduction in root length, a low number of roots per seedling, and a consequent decrease in grain yield.

Seedling Biomass

The results in Table 1 indicated that HT and WL did not affect the seedling biomass of cv. MRIA. It can be concluded that the seed from a mother plant that is treated with high temperature or water stress can survive as well as the seed from a healthy mother plant. It may influence the percentage of germination and cause a delay in seedling establishment, but it does not impact the biomass of the seedlings. The good management of water during seed development also plays a crucial role in influencing the seedling biomass of rice seeds. Jumrani & Bhatia (2018) report the greatest losses in dry matter plants, in contrast to Yanqi (2018) findings, which showed that heat stress causes physiological damage to rice plants by reducing light perception, enzymatic activity, and carbohydrate metabolism, ultimately leading to a decrease in rice growth. Vibhuti et al. (2015) found an inverse relationship between water stress, biomass, and a reduction in shoot dry weight as water stress increased in the Narendra 1 and Sabarmati varieties. However, the Hybrid 312 variety completely inhibited biomass at all stages.

Seedling Vigour Index (SVI)

This study showed that HT lowers the SVI as compared to WL, and this reduction occurred at all stages of seed development. The results demonstrated a significant difference in SVI (2354.15 SVI) between the treated plant and the control plant at 8 DAA (1611.66 SVI), 21 DAA (1721.57 SVI), 14 DAA (1792.80 SVI), and finally at 28 DAA (1802.80 SVI). Like to the other parameters, the susceptibility of seeds to loss of vigor depends on the stage of development. Stress levels of HT and WL during seed development have a substantial impact on seed germination, which can result in a decrease in the vigor index (Begcy et al., 2018). Both HT and WL promote inhibition in leaf and root growth on rice-growing plants. This situation, causes the negative impact to overall seed vigor capacity and later in crop production. However, Yari et al. (2012) suggested that the implementation of thermal hardening methods, for example, starting with chilling treatment followed by heating, can improve germination capacity and the performance of seedling vigor. Furthermore, studies by Yamane et al. (2017) have indicated that maintaining a high seed moisture content under drought conditions can induce key factors during sprouting and is associated with seed vigor in rice.

Amylose Content

The effect of HT and WL on the amylose content (%) of cv. MRIA at different stages of seed development is shown in Fig. 2. Generally, both environmental stresses showed a reduction in amylose content. However, plants exposed to WL showed a higher reduction in amylose content at 8 and 28 DAA than those exposed to HT, although there was no significant difference between them. The current findings reveal that WL significantly influences the amylose content of cv. MRIA, while HT exerts a greater influence. Xu et al. (2022) reported that as the temperature increased, the amylose content, head rice rate, and gel consistency of the rice decreased significantly. Liu et al. (2017) supported this finding, stating that lower environmental temperatures increased the amylose content in non-waxy rice varieties. Gao et al. (2012) showed that HT and drought during the grain-filling stage decreased amylose content but increased protein content in rice. High-temperature stress during the grain-filling stage significantly alters rice grain quality. Studies indicate that for low-amylose varieties, amylose content may slightly increase under heat stress, whereas medium to high-amylose varieties typically experience a decrease (Zhang et al., 2019). Fu et al. (2019) said that HT during seed development, especially during the grain-filling stage, lowers the amount of amylose in rice seeds. This changes the structure of the fine amylopectin and makes the grains chalkier.

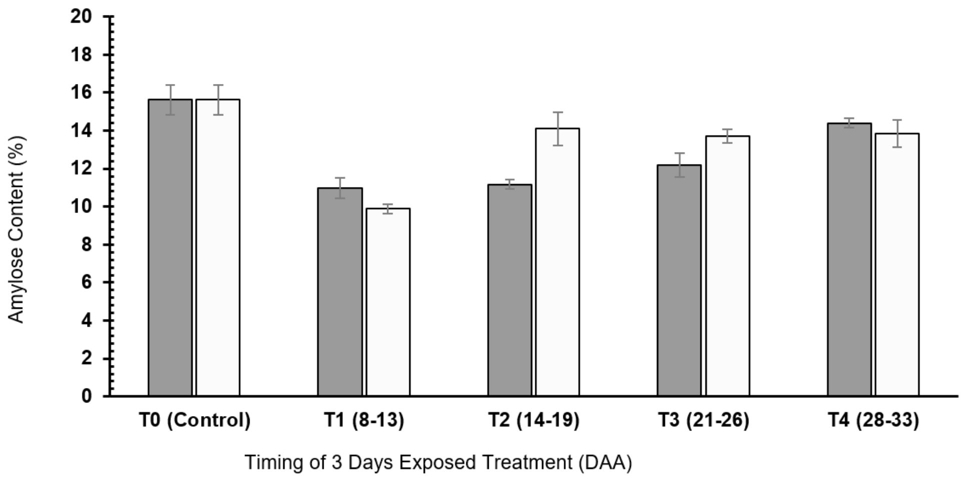
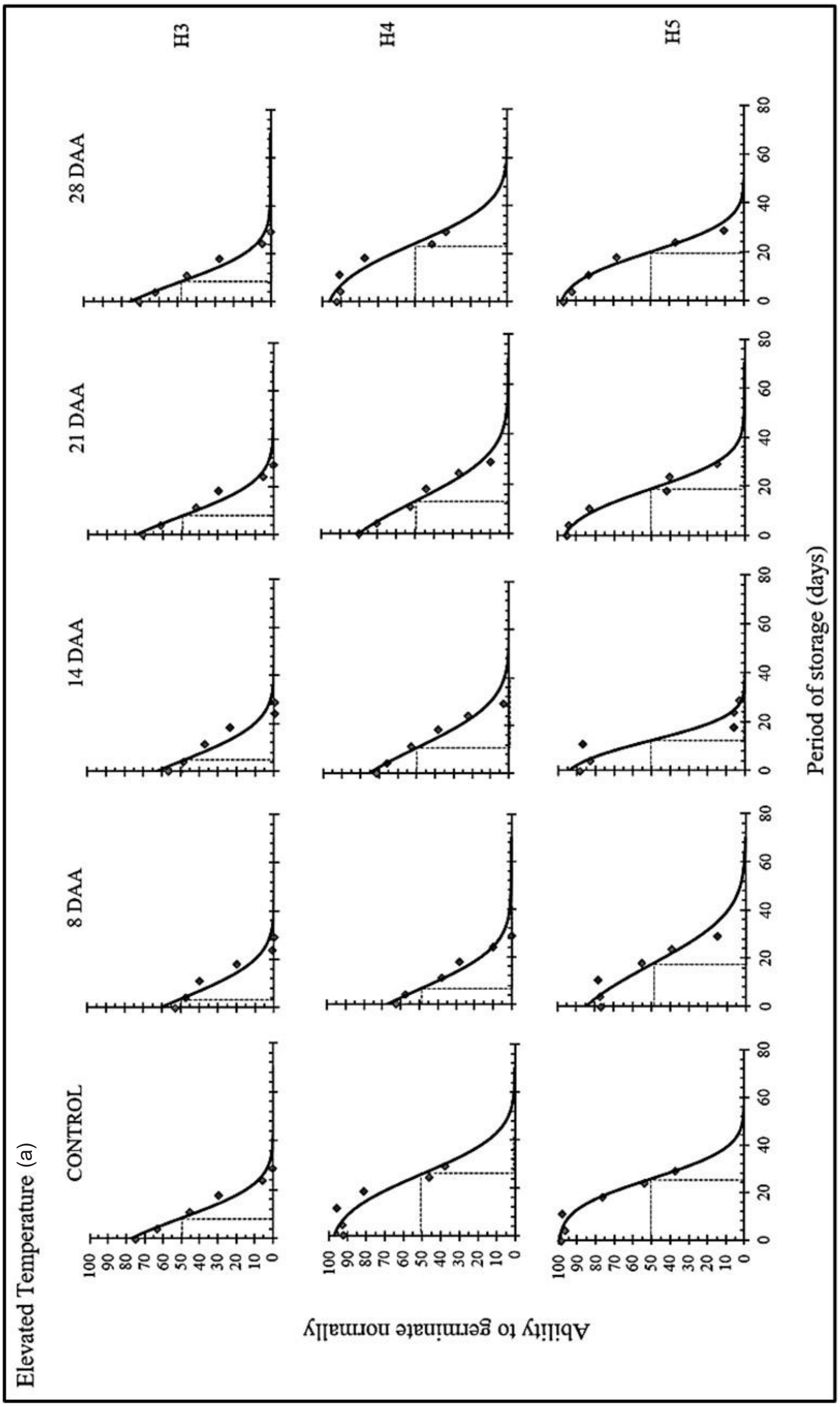


Fig. 2. Concentration of Amylose content (%) of aerobic rice cv. MRIA at harvest maturity (34 DAA) as exposed to HT (28/40 °C) with a 12-h photoperiod and 75±0.5% RH (■) and WL- water limitation (□) for a 3-day period during seed development (8, 14, 21, and 28 DAA).


Elevated Temperature (a)
CONTROL
8 DAA
14 DAA
21 DAA
28 DAA
H3
H4
H5
Ability to germinate normally
Period of storage (days)

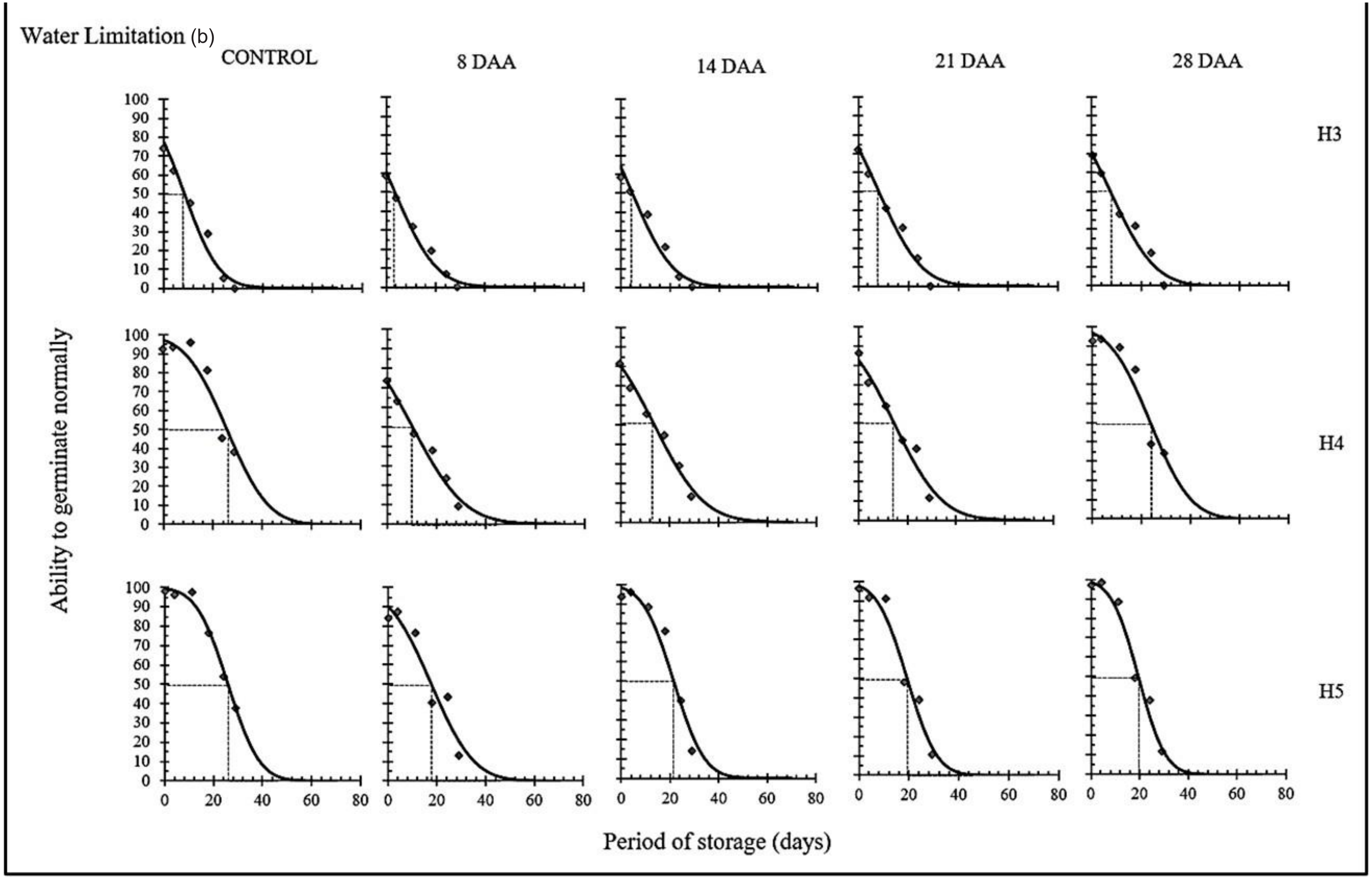


Fig. 3A and 3B: Loss in viability of seeds cv. MRIA harvested serially at 20, 27, 34 DAA (H3, H4 and H5) from plants treated with (A) elevated temperature; (B) water limitation at different stage during seed development (8, 14, 21 and 28 DAA)

Seed Viability Loss

This result indicates that seed viability loss in storage parallels the duration of storage time (Fig. 3A and 3B). Seeds harvested at 27 DAA (H4) exhibited similar viability patterns compared to the control plants. However, when exposed at 8 DAA, the seeds experienced a significantly greater loss of viability. The earliest harvest, at 20 DAA, showed the most pronounced detrimental effect during storage. In contrast, seeds harvested at 34 DAA did not exhibit a detrimental effect to HT (Fig. 3A). In Fig. 3(B), plants treated with WL showed that seeds obtained from plants harvested at 34 DAA were much more resilient to water stress. When exposed to water limitation, seeds harvested at 20 DAA exhibited a significant adverse effect. Seeds harvested at 34 DAA have already completed most of their maturation processes. Mature seeds are often more resilient to environmental stresses compared to seeds shown earlier in development (Abdul Rahman & Ellis, 2019). At the physiological maturity stage, seeds exhibited better tolerance to high temperatures due to their developmental and physiological state at the time of harvest, as well as potential adaptive responses to environmental conditions during plant growth. Seeds also may have sufficient food storage reserves and protective compounds such as antioxidants, which contribute to the seed's ability to withstand elevated temperatures (Debeaujon et al., 2000). Generally, whenever a seed had obtained a quiescent state or dormancy, it was potentially less susceptible to the effects of environmental stressors. In this study, seeds harvested late in seed development (34 DAA) reduced seed metabolic activity as compared to seeds harvested earlier, which could reduce their sensitivity to stressful conditions. In addition, as stated by Bewley et al. (2013), plants that have undergone genetic and epigenetic changes during their development might influence seed resilience to environmental stress. Both types of changes are important in creating an organism's traits, adaptation, and evolutionary processes. Seeds harvested later might inherit traits that enhance seed capability to stress tolerance. As rice plants were exposed to elevated temperatures throughout their development, seeds may have undergone acclimation processes for better tolerance to HT by the time they reached 34 DAA. Fig. 3A and B clearly demonstrate that seeds subjected to elevated temperatures experienced a significant reduction in seed viability performance in storage as compared to plants subjected to WL. In general, WL affects seed viability by limiting the imbibition process and inducing cellular dehydration. Seeds can adapt to stress temporarily, by entered a dormant state or adjusting their metabolism capacity until conditions get into normal condition. This adaptation mechanism allows seeds to withstand WL for longer periods as compared to those caused by HT. Overall, the present study suggests that HT, reduces the seeds' ability to maintain viability or quality rather than WL.

Seed Longevity

Fig. 4A and 4B show the estimated seed longevity period of p50 for seeds of cv. MRIA that were harvested at different times (20, 27, and 34 DAA) while they were growing in controlled conditions for aging. This information was valuable, as it provides a clear indication of the viability of the seed lot when stored at 40°C and 70% relative humidity. Plants treated at HT experience an increase in seed longevity with subsequent harvesting, except for those treated at 21 DAA. The plants treated at 14 DAA had the lowest seed longevity at the last harvesting, 34 DAA, with a p50 value of just 3 days. The longest seed longevity was from seeds with untreated plants, indicating the resilience of the seed lot under the accelerated aging conditions (Fig. 4A). Generally, the present study has shown that seeds harvested later from plants subjected to HT exhibit increased longevity compared to those harvested earlier. As discussed before, seeds harvested later in development often have completed more of their maturation processes, including the accumulation of storage compounds and protective substances. As plants exposed to HT at different stages of seed development induce changes at the genetic level as well as physiological attributes, plant undergo the adaptations process that enhances their ability to tolerate in stressful conditions. In addition, it is also capable of slowing down the seed deterioration and improving seed longevity. The present study demonstrated that treating the rice plant at 14 DAA resulted in a reduction of the (p50) value (Fig. 4A). This indicated that plants treated with HT have shorter seed lifespans when harvested later. In some cases, exposure to HT during seed development can accelerate aging processes in seeds. Even if seed were harvested later, this premature aging can lead to a decrease in seed longevity in storage. While it is possible that seed longevity increases with later harvesting under high-temperature conditions in some cases, it is also important to consider that this relationship is not universal. Harvesting time and stress treatments affect seed longevity, and factors like seed physiology, genetic background, and environmental conditions all play crucial roles.

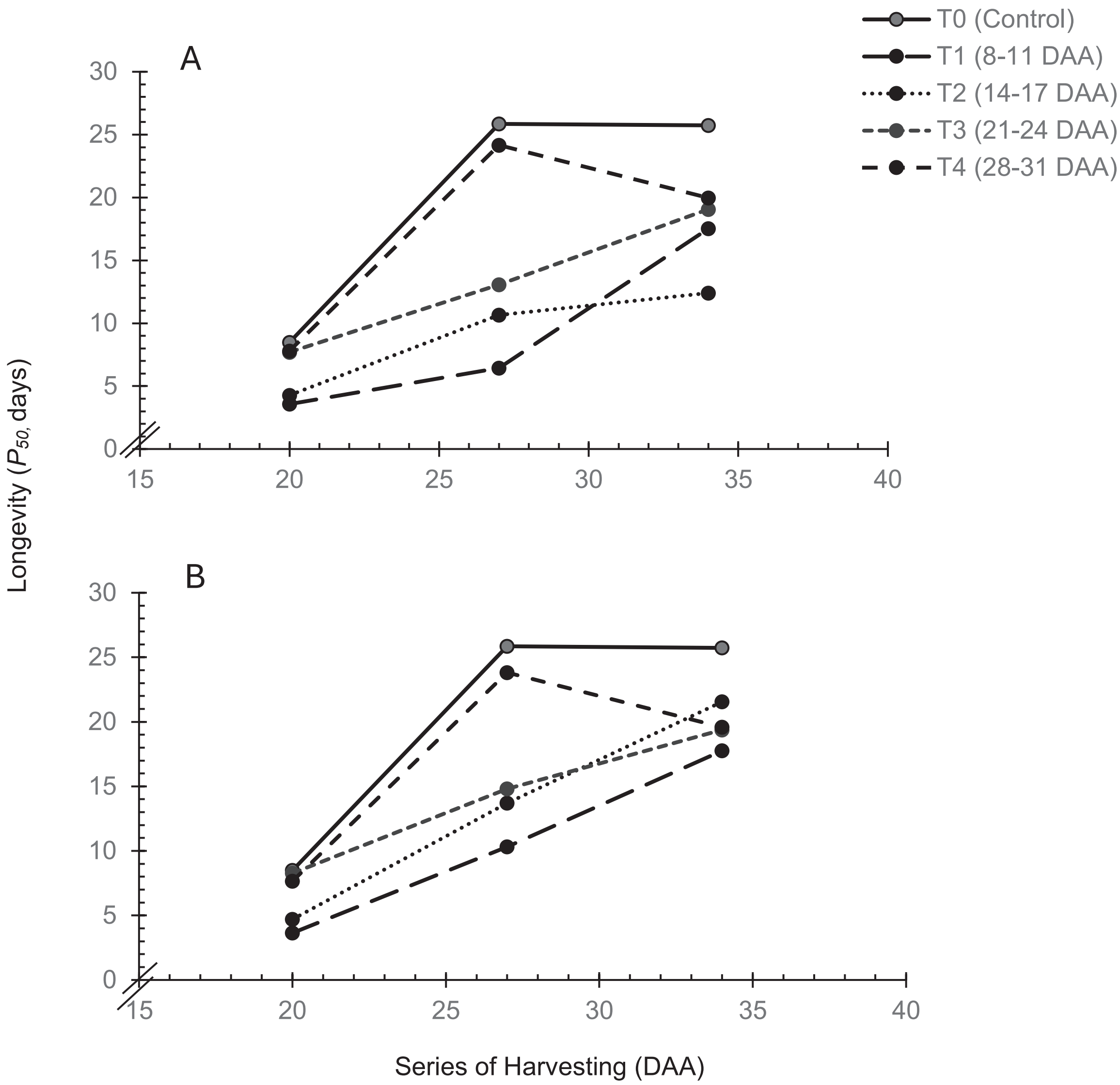


Fig. 4A and 4B. Longevity (*p*50 provided by parameters of seed viability equation fitted by probit analysis) of seeds cv. MRIA harvested serially (20, 27, 34 DAA) during their development from plants treated with (A) elevated temperature, (B) water limitation, and stored hermetically at 40℃, 75% RH with seed storage moisture content at 15%±0.5.

CONCLUSION AND SUGGESTION

Yield and seed quality, including longevity, of aerobic rice cv. MRIA 1 are significantly influenced by high temperature and water limitation during early seed development, with later-harvested seeds show greater longevity.

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