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Effect of Elevated Temperature on the Growth, Physiological, and Yield-Related Traits of Commercial Rice in Malaysia

(Kesan Suhu Tinggi ke atas Pertumbuhan, Fisiologi dan Sifat Berkaitan Hasil Padi Komersial di Malaysia)

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ABSTRACT

Rising temperatures from climate change threaten rice production, impacting livelihoods, global food security, and the sustainability of feeding a growing population. Unlike most studies focusing on specific growth stages, this study investigated the effects of 35 °C (T35) and 36 °C (T36) on the growth, physiological traits across all growth stages and yield-related traits of four Malaysian rice varieties - Sempadan 303 (S303), Sebernas 307 (S307), UKMRC02 (RC02), and UKMC09 (RC09) – compared to MR219, a high-yielding variety. Elevated temperature observed significant differences in plant height (PH), leaf area index (LAI), 100-filled grain weight (100GW), filled grain (FG), grain to leaf area ratio (GToLAI), and several grain nutrients in rice varieties. LAI correlated positively with PH (R^2=0.723**) and stomatal conductance (R^2=0.672**). All varieties recorded higher relative chlorophyll content at 126 days after sowing (DAS) surpassing values at 90 DAS and were significantly higher in T36 for MR219 and S303 showing adaptation to elevated temperature. The harvest index was higher in T36 across all varieties, except RC02, which had a lower FG. All varieties showed no significant difference in Mg, Al, and Si, although MR219 and RC09 had lower P and K in T36. Ca was higher in T36 for all varieties except MR219. This study highlights the varied growth, physiological, and yield-related responses of Malaysian rice varieties to elevated temperatures, with MR219, S303, and RC09 showing strong adaptation due to better stress-coping mechanisms such as maintaining higher LAI, 100GW, HI, and Ca, while S307 and RC02 demonstrated susceptibility.

Keywords: Climate change; increased temperature; Malaysian rice; rice growth; rice yield

ABSTRAK

Peningkatan suhu akibat perubahan iklim mengancam pengeluaran padi, menjejaskan mata pencarian, keterjaminan makanan global dan kelestarian dalam menampung keperluan makanan bagi populasi yang kian meningkat. Berbeza dengan kebanyakan kajian yang memfokuskan peringkat pertumbuhan tertentu, penyelidikan ini mengkaji kesan suhu, 35 °C (T35) dan 36 °C (T36) ke atas morfo-fisologi bagi semua peringkat pertumbuhan dan parameter berkaitan hasil empat varieti padi Malaysia - Sempadan 303 (S303), Sebernas 307 (S307), UKMRC02 (RC02) dan UKMC09 (RC09) – berbanding varieti hasil tinggi MR219. Peningkatan suhu menunjukkan perbezaan signifikan pada ketinggian pokok (PH), indeks keluasan daun (LAI), berat 100 bijirin berisi (100GW), peratus bijirin berisi (FG), nisbah bijirin kepada LAI (GToLAI) dan beberapa nutrien bijirin dalam varieti padi. LAI berkolerasi positif dengan PH (R^2=0.723**) dan konduksian stomata (R^2=0.672**). Semua varieti mencatatkan kandungan klorofil relatif yang lebih tinggi pada 126 hari selepas disemai (DAS) berbanding pada 90 DAS. Peningkatan ini ketara dalam T36 untuk MR219 dan S303, menunjukkan kemampuan adaptasi terhadap pengingkatan suhu. Semua varieti mencatat indeks hasil lebih tinggi dalam T36, kecuali RC02 yang mempunyai FG lebih rendah. Semua varieti tidak menunjukkan perbezaan signifikan kandungan Mg, Al dan Si tetapi MR219 dan RC09 merekod kandungan P dan K lebih rendah dalam T36. Ca lebih tinggi dalam T36 untuk semua varieti kecuali MR219. Kajian ini menekankan pelbagai tindak balas pertumbuhan, hasil dan nutrien varieti padi Malaysia terhadap peningkatan suhu. MR219, S303 dan RC09 menunjukkan adaptasi yang baik melalui mekanisme penyesuaian dengan mengekalkan LAI, 100GW, HI, dan Ca yang lebih tinggi berbanding S307 dan RC02 yang menunjukkan kerentanan.

Kata kunci: Hasil padi; kenaikan suhu; padi Malaysia; pertumbuhan pokok; perubahan iklim

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important cereal grains, feeding more than half of the world's population and contributing significantly to the eradication of hunger and poverty (Sethuraman et al. 2021; Shimoyanagi, Abo & Shiotsu 2021). In addition, to being a major source of calories, rice is regarded as a key source of nutrition containing a variety of vitamins and minerals, including vitamins B and E, thiamine, niacin, calcium, manganese, magnesium, selenium, and iron (Nazir et al. 2021; Senguttuvel et al. 2022). Due to its versatility, this important crop is recognised as an essential source of wealth, economic stability, and regional peace for many rice-producing countries, including Malaysia (Sethuraman et al. 2021).

While rice can be grown in diverse climates (i.e., temperate, tropical, and subtropical), its yield varies greatly at different locations or regions and is vulnerable to unfavourable environmental conditions, making it challenging to sustain high levels of productivity (Rahman & Zhang 2022; Reddy et al. 2021). Recent decades have witnessed a discernible change in the global average temperature, which is projected to have unfavourable climatic occurrences such as an increase in heatwaves, droughts, and floods, which could reduce the rice yield (Tan et al. 2021; Tang 2019). The negative impact of climate change on rice production can lead to a cascading effect on its sustainability, affecting food and nutrition security, as well as the income and well-being of the global population (Sethuraman et al. 2021). This, in turn, has a direct impact on several Sustainable Development Goals (SDGs), such as including SDG1 (No Poverty) and SDG2 (Zero Hunger) (Sethuraman et al. 2021; Xu, Chu & Yao 2021).

Temperature is a key environmental factor that influences crop development and production, with rising temperatures posing direct and indirect challenges to the agriculture sector, affecting food and nutrition security as well as the socioeconomics of many nations, including Malaysia (Tan et al. 2021). Heat stress is an abiotic stress associated with climate change where an increase in temperature beyond the threshold level for an extended period could cause permanent damage to plant growth and development (Kilasi et al. 2018). Because rice cultivation is dependent on climatic cycles and weather patterns, heat stress can have a negative impact on rice production, especially during panicle emergence and flowering stages (Yang, 2018). Elevated temperatures have also been reported to negatively influence grain weight during the heading and grain-filling stages (Shimoyanagi, Abo & Shiotsu 2021; Thuy et al. 2021).

Previous research on the effects of temperature on rice cultivation has primarily focused on specific growth stages such as early growth (Begcy, Sandhu & Walia 2018; Reddy et al. 2021), heading (Wang et al. 2020), flowering (Malini et al. 2023; Shi et al. 2018), or grain filling (Shi et al. 2016; Shimoyanagi, Abo & Shiotsu 2021; Yang 2018). This leaves a gap in understanding how high temperatures affect overall growth, yield, and grain mineral content. The findings of the present study will address that knowledge gap. Four commercial Malaysian rice varieties, namely Sempadan 303, Sebernas 307, UKMRC02, and UKMRC09, were compared to the control variety MR219 in terms of growth and performance under two temperature conditions (35 °C and 36 °C) from germination to maturity. MR219 is a locally developed high-yield rice variety (7 to 10 t ha^{-1}) with an average maturation period of 105 to 111 days. It was the most cultivated variety, accounting for nearly 70% to 90% of local paddy fields since its release in 2001 (NurulNahar et al. 2020; Zuki et al. 2020). However, after years of intensive cultivation, MR219 exhibited a higher disease susceptibility, resulting in yield loss and prompting its discontinuation in 2011. This paved the way for several new improved varieties, including Sempadan 303 and Sebernas 307, with desired traits such as high yield with shorter maturation periods, drought and heat tolerance, and pest and disease resistance (Saad et al. 2021; Sunian et al. 2022).

UKMRC09 (RC09), a low GI red rice variety developed by Universiti Kebangsaan Malaysia (UKM), has a greater yield potential, blast disease resistance, and antioxidant properties compared to MR219 (Nadarajah, Omar & Thing 2014; Se et al. 2016). UKMRC02 (RC02) is high-yielding (12 – 14 t/ha), blast-resistant, and submergence-tolerant, while RC09 is diabetic-friendly because of its low glycemic index and high antioxidant content (Dorairaj & Govender 2023). Although some of these newly released local varieties have agronomic data for the current climate, there is little information on how they will perform in the hotter future climate. Short-term heat stress lasting two to ten days can significantly impact rice yield (Ali et al. 2019; Begcy, Sandhu & Walia 2018; Zhen et al. 2019). Understanding how these commercial rice varieties respond to elevated temperatures would enable more effective rice production in the face of climate change and help close yield gaps, as the country's current rice self-sufficiency is only approximately 70% (Dorairaj & Govender 2023).

This study aimed to examine how elevated temperatures (35 °C and 36 °C) affect growth, physiological traits, and yield-related parameters of four Malaysian commercial rice varieties (Sempadan 303, Sebernas 307, UKMRC02, and UKMRC09) using MR219 as the control. These varieties were evaluated from germination to maturity to compare their growth and performance under these temperature conditions. With climate change-induced heat stress threatening the nation's rice security, understanding the performance of these local varieties under increased temperatures is crucial. By evaluating these factors, the study seeks to provide insights for more effective rice production in the context of climate change, thereby contributing to closing the yield gaps and improving Malaysia's rice self-sufficiency.

MATERIALS AND METHODS

PLANT MATERIALS AND EXPERIMENTAL DESIGN

A greenhouse experiment was conducted in growth chambers at Rimba Ilmu Botanical Garden, Universiti Malaya (UM) (3°7′51.85″N 101°39′28.67″E) from January 2022 to July 2022. Seeds of MR219, S303, and S307 were sourced from the Malaysian Agricultural Research and Development Institute (MARDI), while RC02 and RC09 were obtained from Universiti Kebangsaan Malaysia, Malaysia. Seeds were pre-treated by heating in a 50 °C oven for three days to break seed dormancy (Krishna Jagadish et al. 2011), then germinated and grown to maturity. The experiment used a completely randomised design (CRD) with three biological replicates, resulting in ten treatments across five rice varieties under two elevated temperature conditions; 35 °C (T35) and 36 °C (T36). The elevated temperatures used in this study were based on an average ambient temperature of 34 °C, which was determined prior to the experiment using data from a Petaling Jaya weather station (3°06' N: 101°39' E) recorded by the Malaysian Meteorological Department between 2010 and 2019, corresponding to 1 °C and 2 °C increase above ambient baseline to reflect projected warming trends (Tan et al. 2021). Throughout the experiment, plants were well-watered and fertilised at the recommended rates of 120 kg N/ha, 70 kg P_2O_5/ha, and 80 kg K_2O/ha (Zain et al. 2014).

DATA COLLECTION

Data were collected from all three replicates in all treatments to evaluate the growth, physiological traits, and yield-related parameters of the selected rice varieties. Plant height (PH), measured weekly beginning the first week after sowing, from the ground surface sheath to the uppermost fully developed leaf, corresponding to the vegetative, reproductive, and ripening stages. The leaf area index (LAI) was calculated as 0.75 × leaf length × flag leaf width at harvest (Wang et al. 2020)

Relative chlorophyll content (RCC), stomatal conductance (g_s), chlorophyll A (Chl A), and chlorophyll B (Chl B) were measured at 90 and 126 days after sowing. RCC was quantified using SPAD values with a portable chlorophyll meter (SPAD-520, Plus Milonta Inc, USA). Stomatal conductance, which indicates the rate of carbon dioxide (CO_2) uptake or evaporation, was measured with a leaf porometer (SC-1, Decagon Devices Inc, USA) (Wang et al. 2020). Chl A and Chl B were determined using methods outlined by Swapna and Shylaraj (2017) with minor modifications and measured with a UV-Vis spectrophotometer (Thermo Scientific GENESYS 50, USA). The following formulas were used for calculations:

$$\text{Chlorophyll A} = \frac{12.7(A663) - 2.69\,(A645)}{1000} \times \frac{v}{W}$$

$$\text{Chlorophyll B} = \frac{22.9(A645) - 4.86(A663)}{1000} \times \frac{v}{W}$$

$$\text{Carotenoid} = \frac{A(480) + 114(A663) - 638(A645)}{1000} \times \frac{v}{W}$$

where A is the absorbance; W is the leaf sample weight; and v is the sample volume.

Rice grains were harvested after 70% of the grains turned golden brown. Harvested plants were separated into shoot biomass, which includes tillers, leaf sheaths, and panicles, before being oven-dried at 70 °C for 72 h. Three randomly selected plants had their yield parameters assessed, including harvest index (HI), weight of 100 filled grains (100GW), percentage fill grain (FG), and grain numbers to LAI ratio (GToLAI). Harvest index was calculated as the percent ratio of grain weight to dried shoot biomass (Thuy et al. 2021).

The mineral content in the rice grains was analysed as part of yield attributes (Shimoyanagi, Abo & Shiotsu 2021). At maturity, rice grains were harvested from three randomly selected plants, dried, dehusked and subjected to mineral analysis. Sample from these grains was analysed for magnesium (Mg), aluminium (Al), silicon (Si), phosphorus (P), potassium (K), and calcium (Ca) using ultra-high resolution energy dispersive X-ray spectroscopy (Hitachi UHR FE-SEM, SU8220) at the Department of Chemistry, Universiti Malaya.

STATISTICAL ANALYSIS

Quantitative data were analysed using multivariate analysis of variance (MANOVA) with SPSS Software (Version 28.0.0.0). Mean separation tests between treatments were conducted using the Duncan Multiple Range Test (DMRT) at 5% and 1% level probability. The standard error of the mean was calculated assuming that data were normally distributed and equally replicated. Pearson correlation was carried out and regression graphs were developed for parameters with high correlation coefficients.

RESULTS AND DISCUSSION

EFFECT OF ELEVATED TEMPERATURE ON GROWTH, PHYSIOLOGICAL TRAITS, AND YIELD-RELATED PARAMETERS

This study has shown significant variations in plant growth, physiology, and yield-related parameters among the five selected Malaysian rice varieties as a result of the 1 °C increase. During the vegetative and reproductive stages, almost all varieties were shorter in T36 (Table 1). However, during the ripening stage, pH differed significantly ($p<0.05$), with MR219 and RC09 being 17.0% and 5.5% taller, respectively, compared to their heights in T35 (Table 1). On the other hand, the effect of increased temperature on pH was evident in varieties S307 and RC02, which were 10.7% and 8.6% shorter in T36 compared to T35. Leaf area index measured at harvest significantly differed ($p<0.05$) across all varieties in both temperature treatments (Table 1). The LAI increased for MR219, S303, and RC09 by approximately 44.7%, 24.2%, and 29.2%, respectively, in T36. RC09 consistently exhibited taller plants across all growth stages and the highest LAI at maturity in both treatments, indicating better adaptability to elevated temperatures, which is consistent with Wang et al. (2020), who reported increased LAI in some rice varieties under higher temperatures. The findings for PH and LAI are in line with previous research by Hussain et al. (2019) showing temperature can alter plant development in some rice varieties and they correspond with studies showing that leaf length contributing to LAI is temperature-dependent (Rouan et al. 2018; Stuerz & Asch 2021).

Understanding the correlation between RCC and g_s is crucial for determining how plants respond to environmental factors. Higher RCC corresponds to higher g_s in optimum conditions, indicating efficient photosynthesis (Malini et al. 2023). Stress conditions, such as elevated temperatures, can disrupt this relationship, leading to decreased RCC and g_s levels as plants undergo physiological stress and reduced photosynthesis activity (Caine et al. 2023; Malini et al. 2023). Figure 1 encompasses the plant physiology responses to the 1 °C temperature increase at 90 DAS and 126 DAS, showing significant response variations between treatments. At 90 DAS, MR219 and RC09 exhibited lower RCC at 36 °C, by 2.1% and 5.2%, respectively, while S303 and S307 showed a slight increase of 3.1% and 4.2%, respectively (Figure 1(i)). In contrast, RC02 showed no significant difference, echoing g_s trends recorded at 90 DAS and 126 DAS, except RC02 (Figure 1(ii)). At 126 DAS, RCC surpassed levels observed at 90 DAS for all tested varieties. It was significantly higher in T36 compared to T35 for MR219 and S303, indicating adaptation to elevated temperatures and improved photosynthesis activity at a later growth stage in response to prolonged temperature stress (Kandel 2020).

Variations in Chl A and Chl B play a vital role in plant response to temperature stress, influencing photosynthesis and, ultimately, crop yield. Prolonged heat stress can decrease chlorophyll content in rice plants, impacting their photosynthetic efficiency and affecting assimilating distribution (Jayaraman & Ramachandran 2022; Nguyen et al. 2021; Zahra et al. 2023). Elevated temperatures affected Chl A and Chl B across treatments in this study (Table 2). Notably, MR219 exhibited a significant increase in both Chl A and Chl B content at 90 DAS in T36, suggesting an adaptive mechanism to cope with the elevated temperature (Sanadya et al. 2023). A similar trend was observed in S303 and S307, while RC02 and RC09 showed no significant changes. The observed increase in chlorophyll content in some varieties suggests an enhanced source capacity, enabling the plants to meet the demands of growing sink tissues at elevated temperatures (Sanadya et al. 2023; Zahra et al. 2023). However, by 126 DAS, most varieties showed lower chlorophyll levels in T35 and T36 compared to 90 DAS, likely due to leaf senescence, a natural process where chlorophyll declines as the leaf matures (Rubia et al. 2014). Despite this overall decline, MR219 maintained significantly higher Chl A and Chl B in T36 at 126 DAS than all other varieties, indicating a sustained photosynthetic capacity during the late development stage (Zahra et al. 2023). As rice plants transition to the reproductive stage around 126 DAS, the emphasis shifts towards supporting the reproductive structure, such as grain. MR219's ability to maintain higher chlorophyll content at this stage suggests it may have an advantage in supporting reproductive structures such as grain, even under prolonged heat stress (Sanwong et al. 2023; Yan et al. 2021).

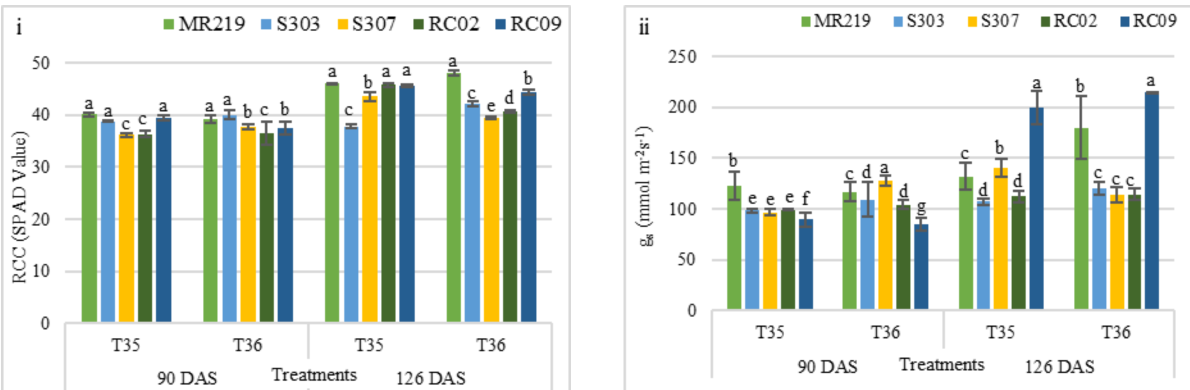
Figure 2(i) - 2(vi) illustrates the response of yield-related parameters of the five rice varieties to the 1 °C temperature increase. Harvest index, which measures biomass conversion efficiency to grain, varies across crops with temperature shifts impairing HI and FG differently (Shimoyanagi, Abo & Shiotsu 2021; Sihag et al. 2024). In our study, all varieties recorded increased HI values at higher temperatures but lower FG. The control variety MR219 exhibited a low HI of 22.7% in T35, increasing to 37.2% in T36 (Figure 2(i)). Despite significant differences in HI and 100GW (Figure 2(iii)), the high GToLAI of MR219 in T36 suggests efficient leaf area to grain production conversion, resulting in balanced growth and yield with no significant differences in FG, DtF, and DtM across treatments. Despite lower PH and LAI potentially limiting photosynthesis and resource allocation efficiency, S303 recorded higher grain yield, suggesting an adaptive mechanism prioritising grain filling over vegetative growth, which was unaffected by the higher temperature (Sanadya et al. 2023).

RC09, despite having higher PH and LAI showed a lower HI (T35:20.4; T36: 36.3), which could be due to its focus on plant growth, resulting in taller plants (Figure 2(i)). Nonetheless, its FG was relatively high at 82.7% in T35 and 79.0% in T36 demonstrating good yield potential despite its growth emphasis (Sanadya et al. 2023). Temperature changes can alter the growth cycle, either extending or reducing the growth period, which in turn affects yield production (Sanwong et al. 2023). While DtF did not differ significantly for M219, S303, and S307, the DtM varied for all varieties except S307 (Figure 2(v) and 2(vi)). Increased temperature led to extended DtM for MR219, RC02 and RC09, which did not affect their HI,

TABLE 1. Plant height at different growth stages and leaf area index at maturity for all five rice varieties investigated in this study

Parameter	Treatment	Rice varieties				
		MR219	S303	S307	RC02	RC09
PH Veg (cm)	T35	38.0 ± 2.7^{b}	37.3 ± 0.9^{b}	32.0 ± 4.0^{c}	37.0 ± 6.1^{b}	45.3 ± 2.4^{a}
	T36	38.0 ± 5.0^{a}	34.3 ± 3.8^{b}	28.0 ± 3.1^{c}	29.7 ± 3.5^{c}	38.3 ± 3.5^{a}
PH Rep (cm)	T35	81. ± 2.7^{b}	74.3 ± 4.2^{c}	67.3 ± 5.6^{d}	72.6 ± 4.3^{c}	88.3 ± 3.8^{a}
	T36	77.0 ± 5.5^{b}	72.3 ± 0.7^{b}	51.6 ± 8.6^{d}	57 ± 7.5^{d}	82.3 ± 3.7^{a}
PH Rip (cm)	T35	88.3 ± 1.8^{c}	83.0 ± 2.7^{d}	84.0 ± 5.5^{d}	90.0 ± 0.0^{b}	102.3 ± 3.4^{a}
	T36	103.3 ± 4.1^{b}	80.0 ± 2.0^{c}	75.0 ± 1.7^{d}	82.3 ± 1.2^{c}	108 ± 1.0^{a}
LAI (cm^2)	T35	38.3 ± 5.3^{c}	33.3 ± 5.4^{d}	40.2 ± 4.4^{b}	40.6 ± 4.6^{b}	48.4 ± 2.3^{a}
	T36	55.3 ± 2.0^{b}	41.4 ± 2.12^{c}	30.9 ± 0.8^{d}	31.0 ± 0.7^{d}	62.2 ± 1.4^{a}

Values are expressed as mean ± standard error mean (N = 30). The mean value followed by different letters within the same row indicates a significant difference according to Duncan's test with alpha = 0.05. Note: 35 °C (T35), 36 °C (T36), Plant height (PH), Vegetative stage (Veg), Reproductive stage (Rep), Ripening stage (Rip), and Leaf area index (LAI)



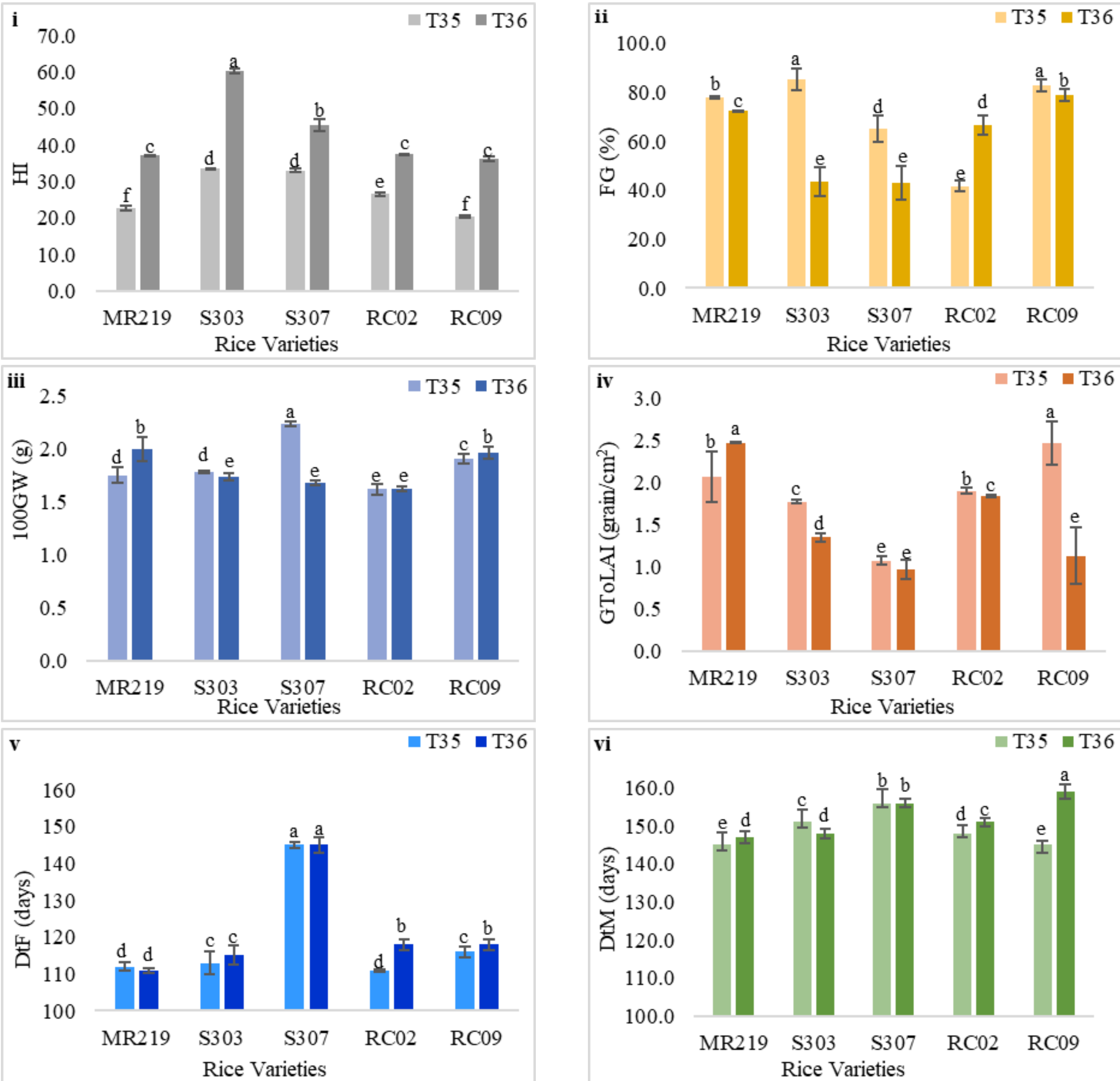
Different letters depict significant differences according to Duncan's Test with alpha = 0.05. Note: 35 °C (T35), 36 °C (T36), Days after sown (DAS)

FIGURE 1. Effect of heat treatments on (i) Relative chlorophyll content (RCC) and (ii) Stomatal conductance (g_s) at 90 DAS and 126 DAS for all five rice varieties in T35 and T36

TABLE 2. Chl A and Chl B content at both 90 DAS and 126 DAS for all five rice varieties investigated in this study

Treatment		Chlorophyll A (mg/mL)					Chlorophyll B (mg/mL)				
		Varieties					Varieties				
		MR219	S303	S307	RC02	RC09	MR219	S303	S307	RC02	RC09
90 DAS	T35	3.89 ± 0.99^{e}	6.26 ± 1.6^{c}	4.96 ± 0.53^{d}	5.81 ± 0.40^{c}	6.26 ± 0.30^{c}	2.73 ± 1.4^{e}	4.44 ± 0.90^{c}	3.48 ± 0.36^{d}	4.15 ± 0.28^{c}	4.45 ± 0.20^{c}
	T36	9.50 ± 1.35^{a}	7.10 ± 0.38^{b}	6.32 ± 0.37^{c}	5.64 ± 0.38^{c}	6.23 ± 0.14^{c}	6.62 ± 0.88^{a}	5.03 ± 0.24^{b}	4.45 ± 0.24^{c}	4.04 ± 0.28^{c}	4.43 ± 0.12^{c}
126 DAS	T35	0.09 ± 0.00^{c}	0.08 ± 0.00^{d}	0.13 ± 0.00^{b}	0.12 ± 0.00^{b}	0.14 ± 0.00^{a}	0.04 ± 0.00^{c}	0.04 ± 0.00^{c}	0.05 ± 0.00^{b}	0.05 ± 0.00^{b}	0.06 ± 0.00^{a}
	T36	0.10 ± 0.00^{c}	0.07 ± 0.00^{e}	0.11 ± 0.00^{c}	0.09 + 0.00^{d}	0.12 ± 0.00^{b}	0.05 ± 0.00^{b}	0.03 ± 0.00^{d}	0.04 ± 0.00^{c}	0.04 ± 0.00^{c}	0.05 ± 0.00^{b}

Values are expressed as mean ± standard error mean (N =30). The mean value followed by different letters within the same row indicates significant difference according to Duncan's test with alpha = 0.05. Note: 35 °C (T35), 36 °C (T36), chlorophyll A (Chl A), and chlorophyll B (Chl B)



35 °C (T35), 36 °C (T36), Harvest index (HI), Fill grain percentage (FG), 100-grain weight (100GW), Grain to Leaf area index ratio (GToLAI), Day-to-flowering (DtF), and Day to maturity (DtM)

FIGURE 2. Effect of heat treatments on (i) HI, (ii) FG, (iii) 100GW, (iv) GToLAI, (v) DtF, and (vi) DtM on all five rice varieties. Mean ± standard error mean. Different letters depict significant differences according to Duncan's Test with alpha = 0.05

with these varieties showing significantly higher HI in T36. Notably, the extended DtM only exhibited higher 100GW for MR219 and RC09, indicating that increased DtM affected the 100GW of RC02. RC02 and RC09 exhibited significant differences in DtF (RC02: 6.3% vs. RC09 1.8%) and DtM (RC02: 2.0% vs. RC09: 9.7%). Delaying the senescence results in insufficient grain filling, with large amounts of carbohydrates remaining unused in the straw (Plaut et al. 2004).

Temperature rise can significantly affect rice's mineral content, a critical yield attribute. This variability potentially threatens global nutrition security due to rice's role as a staple food (Rao et al. 2023; Sanadya et al. 2023). Our study found no significant differences in magnesium (Mg), aluminium (Al), and silicon (Si) between T35 and T36 for all varieties. However, phosphorus (P), potassium (K), calcium (Ca), and iron (Fe) levels varied significantly ($p<0.05$) (Table 3). MR219 had lower P, K, and Ca by 86.4%, 62.7%, and 43.4%, respectively. In comparison, RC09 showed reductions of 60% in P and 47% in K with a 1 °C increase, aligning with Chaturvedi et al. (2017), who reported that increased temperatures of 3 to 4 °C above ambient reduced mineral content in rice grains. This reduction in mineral content is likely due to the impact of decreased g_s, which limits transpiration and impedes the plant's ability to absorb essential minerals (Ouyang et al. 2017). Transpiration acts as a crucial mechanism for the upward movement of nutrients from the soil to plant tissues. This process relies on negative pressure generated by water evaporation from the leaf surface, which draws water and dissolved nutrients into the plant. When g_s is reduced, the mechanism is impaired, disrupting nutrient transport and mineral uptake (Bellasio 2023; Caine et al. 2023). Conversely, heat-tolerance varieties often show higher mineral content with temperature increases during grain filling (Shimoyanagi, Abo & Shiotsu 2021; Wakatsuki et al. 2023). This is congruent with our findings where variety S303 had an increased content of P, K, and Ca, while S307 exhibited higher Mg, P, and Ca (Table 3). Overall, Ca levels increased across all varieties except for MR219, suggesting higher Ca accumulation might be a stress-coping mechanism in response to the elevated temperature, playing a crucial role in stabilizing cell walls and facilitating stress signalling pathways (Pirayesh et al. 2021).

RELATIONSHIP BETWEEN GROWTH, PHYSIOLOGICAL TRAITS, AND YIELD-RELATED PARAMETERS UNDER ELEVATED TEMPERATURE

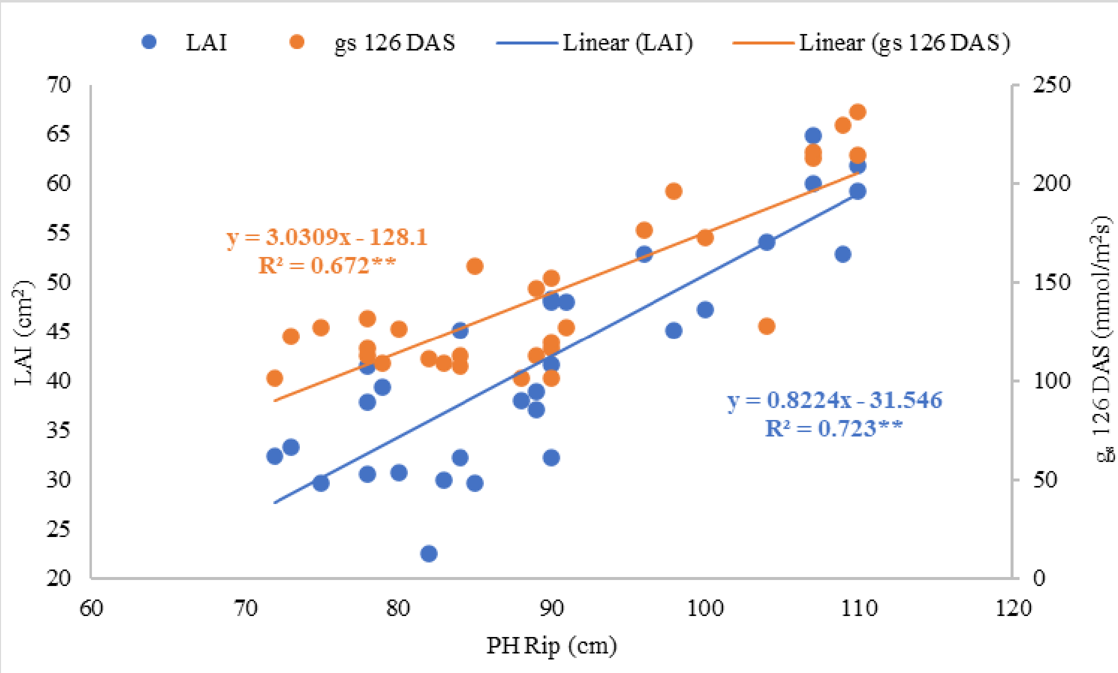
The linear regression analysis showed a positive relationship between LAI and pH ($R^2 = 0.672^{**}$), as well as pH and g_s ($R^2 = 0.723^{**}$), with strong correlations between these parameters (Figure 3 and Supplementary Table S1). The positive relationship between LAI and PH indicates an increase in PH increases the LAI, similar to g_s, which regulates gas exchange in plants and exhibits taller plants as g_s increases. The positive correlation between PH and g_s also suggests efficient stomatal function in the crop, facilitating optimal gas exchange for photosynthesis which contributes towards plant growth and yield production (Li et al. 2022; Yan et al. 2021). In a separate study, Piveta et al. (2020) demonstrated that heat stress did not affect the pH of some rice varieties and found that pH and g_s had a high positive correlation under heat stress indicating higher g_s produced taller plants.

The negative interaction observed between GToLAI and DtM may offer insights into understanding the performance of these rice varieties in response to the increased temperature (Ezin et al. 2022; Sanwong et al. 2023). An R^2 value of 0.479 in this study suggests a moderate inverse correlation between these parameters, with increasing GToLAI resulting in a decrease in DtM with a 1 °C temperature rise (Figure 4). This implies that varieties with higher efficiency leaf-to-grain conversion efficiency tend to mature earlier under elevated temperatures, corresponding to an earlier study by Ezin et al. (2022). MR219 exhibited a significant increase in GToLAI with rising temperatures but showed no significant change in DtM, indicating that temperature elevation did not impact its maturity period. In contrast, S303 and RC09 showed significant decreases in GToLAI, along with corresponding changes in DtM, affecting their maturity. S307's GToLAI and DtM values remained stable across treatments, suggesting a consistent maturity period despite temperature increases. However, RC02, while showing no significant difference in GToLAI, exhibited a notable increase in DtM, indicating delayed maturity under higher temperatures. These findings are also consistent with previous studies by Oliver, Dennis and Dolferus (2007) and Sanwong et al. (2023), which showed contrasting effects of high temperature on rice maturity. Oliver, Dennis and Dolferus (2007) reported delayed maturity, while Sanwong et al. (2023) found early maturity under elevated temperature conditions. Understanding this relationship is

TABLE 3. Effect of heat treatments on mineral content for all five rice varieties investigated in this study

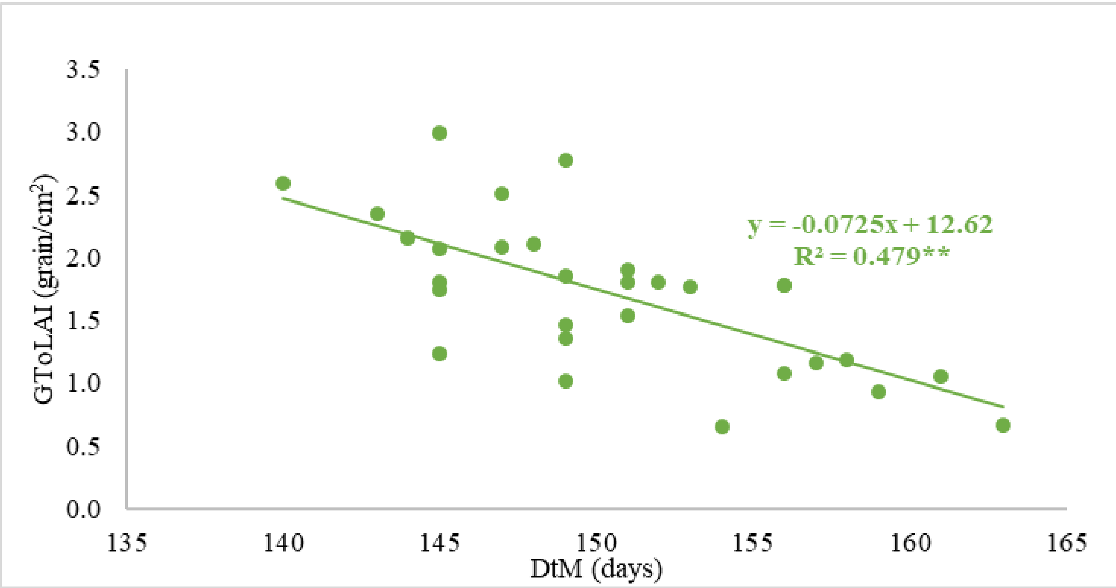
Rice variety	Treatment	Mineral content (keV)						
		Mg	Al	Si	P	K	Ca	Fe
MR219	T35	0.398 ± 0.177^a	0.053 ± 0.039^a	0.030 ± 0.006^a	1.423 ± 0.530^a	0.777 ± 0.265^b	0.053 ± 0.026^c	0.007 ± 0.003^b
	T36	0.260 ± 0.226^a	0.557 ± 0.453^a	0.120 ± 0.110^a	0.193 ± 0.083^c	0.290 ± 0.078^c	0.030 ± 0.010^c	0.007 ± 0.007^b
S303	T35	0.053 ± 0.023^a	0.103 ± 0.009^a	0.020 ± 0.006^a	0.277 ± 0.112^c	0.377 ± 0.086^c	0.033 ± 0.014^c	N.D
	T36	0.187 ± 0.069^a	0.227 ± 0.167^a	0.173 ± 0.079^a	0.500 ± 0.181^c	0.623 ± 0.241^b	0.293 ± 0.145^b	N.D
S307	T35	0.073 ± 0.053^a	0.107 ± 0.034^a	0.063 ± 0.030^a	0.263 ± 0.143^c	0.393 ± 0.181^c	0.07 ± 0.046^c	0.007 ± 0.003^b
	T36	0.107 ± 0.055^a	0.063 ± 0.068^a	0.023 ± 0.013^a	0.373 ± 0.124^c	0.347 ± 0.110^c	0.10 ± 0.060^c	0.007 ± 0.003^b
RC02	T35	0.270 ± 0.051^a	1.597 ± 1.472^a	0.043 ± 0.013^a	0.557 ± 0.389^b	0.657 ± 0.078^b	0.237 ± 0.153^b	0.013 ± 0.009^b
	T36	0.250 ± 0.042^a	0.093 ± 0.047^a	0.097 ± 0.022^a	0.480 ± 0.304^c	0.613 ± 0.231^b	0.433 ± 0.092^a	0.017 ± 0.003^b
RC09	T35	0.390 ± 0.062^a	0.277 ± 0.102^a	0.104 ± 0.054^a	1.427 ± 0.386^a	1.057 ± 0.282^a	0.087 ± 0.042^c	0.007 ± 0.007^b
	T36	0.293 ± 0.079^a	0.267 ± 0.122^a	0.130 ± 0.071^a	0.573 ± 0.141^b	0.56 ± 0.050^b	0.467 ± 0.154^a	0.020 ± 0.010^a

Values are expressed as mean ± standard error mean (N = 30). The mean value followed by different letters within the same row indicates significant differences according to Duncan's Test with alpha =0.05. Note: 35 °C (T35), 36 °C (T36), N.D(not detected)



N = 30, ** = significant at 1%, Plant height at ripening stage (PH Rip), Leaf area index (LAI), Stomatal conductance measure at 126 DAS (g_s 126 DAS), and Days after sown (DAS)

FIGURE 3. Linear regression analysis. The solid lines depict the regression between LAI, PH Rip, and g_s 126 DAS. Regression equations and correlation coefficient (R^2) are included in the plot



N = 30, ** = significant at 1%, Grain to Leaf area index ratio (GToLAI), and Days to maturity (DtM)

FIGURE 4. Linear regression analysis. The solid lines depict the regression between GToLAI and DtM. Regression equations and correlation coefficient (R^2) are included in the plot

crucial for predicting and managing crop maturity under changing environmental conditions induced by increased temperatures in the local context, which could facilitate the optimization of yield production strategies in rice cultivation.

CONCLUSIONS

In conclusion, this study emphasizes the different effects of rising temperatures on Malaysian rice varieties, showcasing a range of responses that underscore their varying adaptability and performance under such conditions. In comparison to other selected varieties, MR219, S303, and RC09 were shown to be able to tolerate temperatures of 36 °C based on multiple growth and yield parameters, including the LAI, 100GW and HI while varieties S307 and RC02 showed susceptibility to the increased temperature. The increase in temperature also resulted in varied mineral content responses, with S303 and RC09 exhibiting the highest Ca accumulation and demonstrating tolerance to the elevated temperature. With global temperatures predicted to rise, understanding the varietal responses of these Malaysian rice varieties is imperative for developing strategies to mitigate climate change's impact on Malaysia's rice nutrition and food security. These findings underscore the urgency of implementing tailored adaptation strategies to ensure the sustainability of rice production and to secure food resources for future generations.

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SUPPLEMENTARY TABLE S1. Pearson's correlation coefficient of parameters measured in this study

	PH Veg	PH Rep	PH Rip	LAI	HI	100GW	FG	GToLAI	DtF	DtM	RCC $_{90DAS}$	RCC $_{126DAS}$	$g_{s\,90DAS}$	$g_{s\,126DAS}$	Chl A $_{90DAS}$	Chl B $_{90DAS}$	Chl A $_{126DAS}$	Chl B $_{126DAS}$	Mg	Al	S	P	S	K	Ca	Fe
PH Veg	1																									
PH Rep	.490**	1																								
PH Rip	.565**	.630**	1																							
LAI	.489**	.549**	.851**	1																						
HI	-.390*	-.398*	-.416*	-0.101	1																					
100GW	0.079	0.249	0.349	.446*	-0.106	1																				
FG	.488**	.401*	.488**	0.335	-.530**	0.326	1																			
GToLAI	.473**	.409*	.367*	0.138	-.483**	-0.086	0.347	1																		
DtF	-.400*	-.488**	-.404*	-0.239	0.203	0.325	-0.263	-.621**	1																	
DtM	-.439*	-.392*	-0.141	-0.001	0.245	0.295	-0.084	-.692**	.512**	1																
RCC $_{90DAS}$	0.228	0.304	0.060	0.127	0.065	-0.064	0.175	0.286	-0.336	-0.316	1															
RCC $_{126DAS}$	.434*	.516**	.666**	.619**	-.418*	0.306	0.113	.469**	-0.333	-.373*	0.125	1														
$g_{s\,90DAS}$	-0.195	-0.354	-.378*	-.374*	0.213	-0.271	-0.230	0.025	0.121	-0.222	0.057	-0.059	1													
$g_{s\,126DAS}$	.436*	.462*	.820**	.762**	-0.251	.475**	.429*	0.222	-0.131	0.043	0.192	.520**	-0.244	1												
Chl A $_{90DAS}$	0.069	0.027	0.322	.467**	0.316	0.158	-0.028	0.147	-0.129	-0.074	0.116	0.148	0.005	0.238	1											

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Chl B 90DAS	0.062	0.022	0.320	.465**	0.322	0.148	-0.033	0.146	-0.139	-0.066	0.107	0.139	-0.009	0.227	.999**	1										
Chl A 126DAS	0.304	0.228	.522**	.364*	-.644**	0.330	0.167	0.067	0.226	0.138	-0.220	.440*	-.409*	.498**	-0.095	-0.096	1									
Chl B 126DAS	0.336	0.279	.593**	.417*	-.638**	0.259	0.197	0.142	0.101	0.113	-0.174	.449*	-.447*	.539**	-0.030	-0.028	.978**	1								
Mg	0.045	0.201	0.289	0.324	-0.291	-0.002	0.143	.391*	-0.336	-0.147	0.265	.412*	-0.150	0.233	0.157	0.173	0.173	0.234	1							
Al	0.319	-0.025	0.086	0.195	-0.120	-0.100	-0.097	0.225	-0.182	-0.112	-0.155	0.246	0.034	-0.016	0.163	0.170	0.191	0.194	0.258	1						
Si	0.107	0.134	0.229	0.343	0.280	0.176	-0.092	-0.031	-0.142	0.099	0.277	0.220	-0.318	.383*	0.316	0.307	-0.031	0.031	0.094	-0.117	1					
P	0.113	.411*	0.244	0.114	-.406*	-0.034	0.143	0.292	-0.196	-0.298	0.211	0.273	-0.199	0.169	-0.130	-0.125	0.219	0.261	.643**	-0.153	0.022	1				
S	-0.070	0.054	0.153	0.077	-0.075	-0.177	-0.024	-0.076	-0.237	0.323	0.007	0.016	-.433*	0.144	-0.164	-0.151	0.114	0.225	0.311	-0.214	.490**	0.269	1			
K	0.086	0.290	0.232	0.156	-0.296	-0.089	0.021	0.220	-0.256	-0.207	0.167	0.200	-.370*	0.186	-0.084	-0.072	0.219	0.273	.605**	-0.065	0.253	.829**	.453*	1		
Ca	-0.139	-0.173	0.050	0.167	0.252	-0.185	-0.169	-0.261	-0.113	0.346	-0.033	-0.047	-.401*	0.083	-0.036	-0.020	-0.028	0.039	0.193	-0.137	.486**	-0.069	.722**	0.148	1	
Fe	-0.256	0.046	0.141	0.146	0.005	-0.014	-0.139	0.052	-0.003	0.158	-.386*	0.178	-0.120	0.093	-0.012	0.004	0.103	0.137	.426*	0.089	0.008	0.289	0.260	0.118	0.288	1

* = significant at 5%, ** = significant at 1%, Plant height (PH), Vegetative stage (Veg), Reproductive stage (Rep), Ripening stage (Rip), Leaf area index (LAI), Harvest index (HI), 100-filled grain weight (100GW), Filled grain (FG), Grain to Leaf area index ratio (GToLAI), Days to flowering (DtF), Days to maturity (DtM), Relative chlorophyll content (RCC), Stomatal conductance (g_s), Chlorophyll A (Chl A), Chlorophyll B (Chl B), Days after sown (DAS), Magnesium (Mg), Aluminium (Al), Silicon (Si), P (Phosphorus), Potassium (K), Calcium (Ca) and Iron (Fe)