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RESEARCH ARTICLE

Individual and concurrent effects of heat and drought stress on the growth and yield of two Malaysian rice cultivars

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ABSTRACT

Heat and drought stress, which often co-occur due to water evaporation, are two major abiotic factors limiting the production of rice (*Oryza sativa* L.) It is crucial to enhance understanding of the effects of these abiotic stresses in rice, particularly for rice-producing countries like Malaysia, which has yet to achieve rice self-sufficiency. This greenhouse study was conducted to evaluate the morphological changes of two important Malaysian cultivars ('MR219' and 'MR303') at vegetative, reproductive, and ripening stages, as well as their physiological response and yield components under normal (control), heat, drought, and combined heat-drought stress conditions. Individual heat stress greatly influenced rice growth and yield, with significant differences ($p < 0.01$) observed across all examined parameters except the grain to leaf area index ratio (GtoLAI). Conversely, individual drought stress mostly affected yield-related parameters, with significant differences ($p < 0.01$) in grain weight (GW), harvest index (HI), and percentage of filled grain (%FG). Interestingly, the combined stresses in this study did not significantly affect plant height (PH) for all growth stages and most yield-related traits (HI, GW, and GtoLAI). The majority of the significant changes ($p < 0.01$) were observed on physiological traits, including chlorophyll *a* (Chl A) and *b* (Chl B). We found a positive correlation between HI and %FG ($R^2 = 0.3974$**) under heat and drought stress, indicating that improving either of these traits can boost rice production. Collectively, our study revealed that the individual effects of heat and drought on rice growth and yield can differ from the effects of combined stress.

Key words: Abiotic stress, climate change, morpho-physiological traits, *Oryza sativa*, and rice production.

INTRODUCTION

Agriculture and climate change are inextricably intertwined, with the latter being the primary driver of climatic stresses that negatively impact agriculture, jeopardising crop productivity and food security on a global scale (Nugroho et al., 2023). Crop research in recent decades has mostly focused on improving the production of three major cereal grain crops: Rice (*Oryza sativa* L.), maize (*Zea mays* L.), and wheat (*Triticum aestivum* L.) (Mohd Hanafiah et al., 2020). Among these crops, rice requires significantly more water to grow and is typically vulnerable to water scarcity due to its semi-aquatic nature (Oladosu et al., 2020). Rice is predominantly grown in flooded lowland ecosystems in Asia and requires 3000 to 5000 L water for every kilogramme of grain produced (Chaudhary et al., 2023). As global warming exacerbates abiotic stresses, many rice-growing countries in Asia, including Malaysia, are becoming increasingly concerned about the production of this vital crop that underpins financial stability and economic development at the local and regional levels (Zhang et al., 2023).

Rice, or crop plants in general, can maintain a delicate balance in optimal development and productivity under normal environmental conditions. Nonetheless, under climatic stresses, most crops encounter physiological as well as biochemical challenges, causing growth disruption due mainly to impaired primary metabolism (Kumari et al., 2022). Drought and heat are currently two of the most significant abiotic factors that co-occur and affect rice growth and development worldwide (Yadav et al., 2022; Ren et al., 2023). Similar weather circulation irregularities that are aggravated by interactions with soil moisture and different atmospheric components are often the cause of both droughts and heat waves. Frequent hot weather affects precipitation, accelerating soil water evaporation and increasing drought risk (Yu et al., 2023). Drought stress has affected more than 60% of the world's rice cultivation area, with developing and developed countries making up roughly 33% and 42% of that total, respectively (Heredia et al., 2022). Heat stress, on the other hand, has been associated with a 6%-10% reduction in rice yield for every 1 °C increase in average temperature (Ren et al., 2023). It is predicted that drought and heat stress will increase to a greater extent in tropical and subtropical regions, which are the primary rice producing areas (Williams et al., 2024).

Studies have shown that plants respond differently to multiple abiotic stresses and that inferences or conclusions regarding the responses of combined stresses should not be drawn from investigating individual stresses (Ramegowda et al., 2024). Heat stress, whether alone or in combination with drought stress, has been reported to raise plant tissue temperatures and interfere with critical physiological functions such as respiration and photosynthesis (Yousaf et al., 2022). In the case of rice, heat stress affects its lifecycle mainly through increasing spikelet sterility and shortening grain filling, both of which reducing grain yield. Grain yield can be completely nullified in severe condition (Shrestha et al., 2022). To date, drought and heat stress responses in rice have mostly been studied independently (Xu et al., 2021; Ren et al., 2023). According to Yadav et al. (2022), rice has a unique response to stress combinations such as drought, heat, and salinity, with physiological and molecular adaptation. Although the significance of combined stress in rice has been recognised in recent years, a deeper understanding of how the crop responses to multiple stresses concurrently is essential as climate change intensifies (Ramegowda et al., 2024).

As climate change is expected to increase the frequency of heat and drought stress co-occurrences, understanding how these stresses—both individually and in combination—affect rice development and yield is crucial, which is especially relevant for countries like Malaysia that have not achieved rice self-sufficiency, with rice production constantly influenced by multiple climatic factors (Carins-Murphy et al., 2023; Dorairaj and Govender, 2023; Xu et al., 2023). This study was conducted to examine how two important commercial Malaysian rice cultivars (MR219 and MR303) responded to individual and combined effects of heat and drought at different growth stages. We hypothesized that the combined drought and heat stress alters rice growth and negatively impacts its yield, with a different effect than either of drought and heat stress alone. The acquired knowledge will serve as the foundation for the sustainable cultivation of commercial Malaysian rice cultivars in the face of climate change, increasing rice self-sufficiency while also contributing to several Sustainable Development Goals, most notably Goal 2 (Zero Hunger) and Goal 13 (Climate Action).

MATERIALS AND METHODS

Plant materials

Two important commercial Malaysian rice (*Oryza sativa* L.) cultivars, MR219 and MR303 (or Sempadan 303), acquired from the Malaysian Agriculture Research and Development Institute (MARDI), were evaluated. 'MR219' is a high-yielding rice with a short maturation period of 105 to 111 d. Since its released in 2001, 'MR219' was planted in approximately 70% to 90% of local paddy fields. However, it was discontinued in 2011 due to worsening disease susceptibility, which resulted in yield losses (Zuki et al., 2020; Dorairaj and Govender, 2023). This contributed to the widespread cultivation of 'MR303', a recently developed cultivar with advantageous characteristics such as resistance to heat, drought, pests, and diseases, as well as a high yield with accelerated maturation (Zainol et al., 2023).

Experimental design and growth conditions

Rice plants were grown in pots in growth chambers with controlled conditions at the greenhouse of the Rimba Ilmu Botanical Garden, Universiti Malaya (3°7′51.85″ N, 101°39′28.67″ E) from March to July 2023 (Figure 1). Seeds were pre-treated for 72 h in a 50 °C oven before germination and transplanting to the greenhouse. Five seeds were sown in each pot and thinned to three per pot 14 d after sowing (DAS). This factorial experiment was arranged in complete randomized design (CRD) replicated three times, with three factors: Heat stress (34 [ambient as control], 35, and 36 °C), rice cultivars or genotypes (MR219 and MR303), and drought (well-watered throughout the growth cycle [as control], cyclic water stress for 5, 10, and 15 d). The plants were subjected to their respective cyclic-water stresses from 58 to 120

DAS. Plants were then well-watered from 121 DAS onwards (Figure 1). The absolute control in this study was the local 'MR219' grown at 34 °C without cycling water stress according to standard local farming practices. Plants were fertilised at the recommendation rate of 120 kg N ha^{-1}, 70 kg P_2O_5 ha^{-1}, and 80 kg K_2O ha^{-1} (Zain et al., 2014). The relative humidity ranged between 50% and 60%, with an average atmospheric pressure of 1013 kPa throughout the experiment.

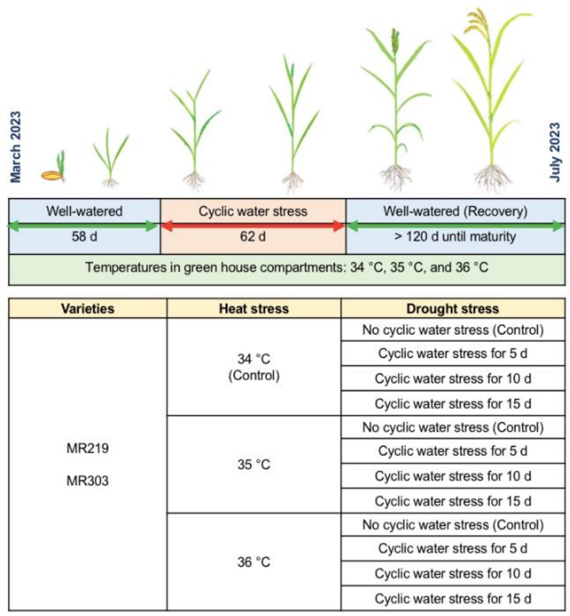

Figure 1. Detailed representation of experimental design.

Data collection

The growth and yield parameters were recorded from all three plants per treatment. Plant height (PH) was measured weekly from the ground surface to the uppermost fully developed leaf. At maturity, leaf area index (LAI) was calculated as 0.75 × leaf length × leaf width (Wang et al., 2020). For yield parameter analysis, three plants from each replicate were randomly sampled and harvested at maturity. Harvested plants were oven dried for 72 h at 70 °C and the weight of 100 full grains (GW) was determined. The harvest index (HI) was calculated as the percent ratio of grain weight and the dried shoot biomass (Thuy et al., 2021). The percentage of filled grain (%FG) and grain to leaf area index ratio (GtoLAI) were calculated.

The in-situ chlorophyll content (SPAD value) was measured 50 DAS using a portable chlorophyll metre SPAD-520Plus (Konica Minolta, Tokyo, Japan). A leaf porometer SC-1 (Decagon Devices Inc., Pullman, Washington, USA) was used to measure stomatal conductance, which represents the rate at which carbon dioxide (CO_2) enters or evaporates (Wang et al., 2020). The major green pigments chlorophyll *a* (Chl A) and chlorophyll *b* (Chl B), and carotenoid content were determined using a UV-Vis spectrophotometer (GENESYS 50, Thermo Scientific, Waltham, Massachusetts, USA), based on procedures by Swapna and Shylaraj (2017) with minor modifications, and calculated using the following formulas:

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

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

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

where A is absorbance, W is leaf sample weight, v is sample volume.

Statistical analysis

Multivariate analysis of variance (MANOVA) was used to analyse collected data using SPSS software (Version 28.0.0.0; IBM, Armonk, New York, USA). The significant parameters were subsequently examined for the mean difference between treatments using Duncan multiple range test (DMRT) at the 5% and 1% probability levels. The standard error of the mean was calculated using the assumption that the data was evenly replicated and normally distributed. Correlation analysis was performed using the standard statistical approach (Anwarmalik et al., 2007), and the three parameters with the highest significant correlation coefficient efficiency were selected for regression analysis.

RESULTS AND DISCUSSION

Individual effects of heat and drought stress on the growth and yield of rice

Among various crop phenotypes, PH and LAI have been identified as the primary indicators of climatic stress, notably drought (Evamoni et al., 2023). Our study revealed significant differences ($p < 0.01$) in PH of all three growth stages and LAI for rice plants grown under heat stress, but nonsignificant differences were found for these traits under drought stress, with the exception of PH during reproductive stage (Table 1). Similar findings were observed for physiological traits. There were significant differences ($p < 0.01$) in all physiological traits examined across heat stress treatments, indicating that heat stress could trigger a series of morpho-physiological changes in local rice varieties. Yousaf et al. (2022) reported that heat stress can increase the temperature of plant tissues and interfere with important physiological processes such as photosynthesis and respiration. In contrast, all physiological traits, with the exception of Chl *b*, did not differ significantly across drought stress treatments (Table 1). According to Das et al. (2024), rice genotypes that are tolerant to deficit soil moisture conditions may have better physiological traits, and 'MR219' and 'MR303' in this study could potentially be such genotypes. Notably, this study observed genotype-dependent trends in all physiological traits ($p < 0.01$ or $p < 0.05$), except for Car, when comparing two individual stress groups (Table 1). These results are in line with those of Lin et al. (2018) and Liu et al. (2019).

Table 1. A three-way ANOVA showing significant levels for growth and yield-related parameters between two rice cultivars grown under different treatments of individual heat and drought stress. *Significant at 5% level; **significant at 1% level; ^{ns}nonsignificant difference; veg: vegetative; rep: reproductive; rip: ripening; PH: plant height: LAI: leaf area index; SPAD value: in-situ chlorophyll content; g_S: stomatal conductance; Chl A: chlorophyll *a* content; Chl B: chlorophyll *b* content; Car: carotenoid content; HI: harvest index; GW: 100 grain weight; %FG: fill grain percentage; GtoLAI: grain to LAI ratio.

Parameter		PH			LAI	SPAD value	g_S	Chl A	Chl B	Car	HI	GW	%FG	GtoLAI
Factor	dF	veg	rep	rip										
		cm			cm^2		$mmol\ m^{-2}\ s^{-1}$	$mg\ mL^{-1}$	$mg\ mL^{-1}$	$mg\ mL^{-1}$		g	%	$spikelets\ cm^{-2}$
Cultivar	1	28.307^{**}	56.277^{**}	66.641^{**}	79.208^{**}	48.092^{**}	10.607^{**}	4.476^{*}	7.152^{**}	0.772^{ns}	2.632^{ns}	0.008^{ns}	3.069^{ns}	19.117^{**}
Heat	3	47.977^{**}	108.220^{**}	92.501^{**}	29.473^{**}	50.087^{**}	52.849^{**}	17.700^{**}	53.587^{**}	9.345^{**}	23.191^{**}	8.208^{**}	28.279^{**}	2.830^{ns}
Drought	3	2.80^{ns}	5.277^{*}	1.998^{ns}	0.960^{ns}	2.74^{ns}	1.435^{ns}	0.192^{ns}	5.388^{**}	2.391^{ns}	4.583^{**}	8.284^{**}	7.663^{**}	1.377^{ns}

By and large, it has been extensively reported that heat and drought stress adversely affect crop yields (Yadav et al., 2022; Ren et al., 2023). This is evident in the current study, as rice plants grown under both heat and drought stress showed significant differences ($p < 0.01$ or $p < 0.05$) in all yield-related traits, except for GtoLAI (Table 1). These stresses, whether individual or combined, have a significant impact on seed yields by reducing seed number and size, ultimately compromising the commercial trait 100-grain weight and seed quality (Sehgal et al., 2018). Their concurrent effects on the morpho-physiology and yield components of Malaysian rice will be discussed in the following section.

Concurrent effects of drought and heat stress on the growth and yield of rice

Regardless of genotype, we found nonsignificant differences in any evaluated growth parameters in rice plants grown under combined heat and drought stress (Table 2). This is in contrast with our results for individual stress, particularly heat stress, which was found to affect PH significantly across all growth stages (Table 1). According to Ramegowda et al. (2024), plants may respond uniquely or differently to multiple abiotic stresses, and investigating individual stresses should not lead to inferences or conclusions about their responses of combined stress.

Table 2. A three-way ANOVA showing significant levels for growth and yield-related parameters between two rice cultivars grown under different treatments of combined heat and drought stress. *Significant at 5% level; **significant at 1% level; ^{ns}nonsignificant difference; veg: vegetative; rep: reproductive; rip: ripening; PH: plant height: LAI: leaf area index; SPAD value: in-situ chlorophyll content; g_S: stomatal conductance; Chl A: chlorophyll *a* content; Chl B: chlorophyll *b* content; Car: carotenoid content; HI: harvest index; GW: 100 grain weight; %FG: fill grain percentage; GtoLAI: grain to LAI ratio.

Parameter		PH			LAI	SPAD value	g_S	Chl A	Chl B	Car	HI	GW	%FG	GtoLAI
Factor	dF	veg	rep	rip										
		cm			cm^2		$mmol\ m^{-2}\ s^{-1}$	$mg\ mL^{-1}$	$mg\ mL^{-1}$	$mg\ mL^{-1}$		g	%	$spikelets\ cm^{-2}$
Cultivar × Heat	2	1.907^{ns}	3.439^{*}	9.950^{**}	3.429^{*}	4.499^{*}	0.776^{ns}	9.760^{**}	15.627^{**}	11.408^{**}	8.118^{**}	1.760^{ns}	23.733^{**}	1.608^{ns}
Heat × Drought	6	0.637^{ns}	0.525^{ns}	1.308^{ns}	0.973^{ns}	1.808^{ns}	2.259^{ns}	6.892^{**}	4.194^{**}	2.810^{*}	1.336^{ns}	1.167^{ns}	2.749^{*}	0.497^{ns}
Cultivar × Drought	3	3.728^{*}	3.687^{*}	1.315^{ns}	0.433^{ns}	9.441^{**}	4.548^{*}	3.738^{*}	2.232^{ns}	5.030^{**}	4.173^{*}	8.634^{**}	0.563^{*}	1.756^{ns}
Cultivar × Drought × Heat	6	0.159^{ns}	0.301^{ns}	0.598^{ns}	0.195^{ns}	2.543^{*}	3.583^{**}	6.692^{**}	3.368^{**}	1.555^{ns}	3.011	1.976^{ns}	2.206^{ns}	1.216^{ns}

On the other hand, all physiological traits examined in this study, except for stomatal conductance g_S, exhibited significant differences ($p < 0.01$ or $p < 0.05$) under combined heat and drought stress (Table 2). It has been reported that heat stress, either alone or in combination with drought stress, could increase the temperature of plant tissues and impede their vital physiological processes (Yousaf et al., 2022). Our investigation also revealed that g_S, Chl A, and Chl B differed significantly ($p < 0.01$) when genotype interaction was present (Table 2), suggesting that these traits are genotype dependent. Yadav et al. (2022) reported that rice has a distinct or unique physiological and molecular response to stress combinations such as heat, drought, and salinity.

Although yield-related traits in this study showed significant differences ($p < 0.01$ or $p < 0.05$) in response to individual heat and drought stress (Table 1), the combination of the two stresses revealed nonsignificant changes in HI, GW, and GtoLAI (Table 2). The HI and GW are two frequently used parameters to determine resource-use efficiency (Yang and Zhang, 2023), and Figure 2 depicts whether different cyclic water stress conditions affect these traits in selected varieties across all three temperature settings. As the cyclic water stress intensified with longer intervals between irrigations, there was a general tendency of reducing HI for 'MR219' across different temperature settings, but 'MR303' had a variable HI response. For GW, 'MR219' displayed a varied pattern when subjected to different cycle water stress and temperatures, whilst 'MR303' did not show any significant change in weight except under 35 °C (Figure 2). This validates the findings of Ramegowda et al. (2024), which demonstrated that plants respond differently to multiple abiotic stresses (such as heat and drought) and that predicting how plants would respond to combined stresses should not be based on the study of individual stresses. On the other hand, %FG differed significantly ($p < 0.05$) under combined stress (Table 2). It has been reported that climatic stress, particularly heat stress, impacts the rice lifecycle primarily by increasing spikelet sterility and reducing grain filling, and that under severe conditions, grain production can be completely nullified (Shrestha et al., 2022).

Relationship between rice growth and yield parameters under drought and heat stress

We conducted correlation analysis (Table 3), and the growth and yield parameters with the highest significant correlation coefficient efficiency were selected for regression analysis (Figure 3). The PH at ripening stage was positively correlated with LAI (Figure 3a), SPAD value (Figure 3b), and g_S (Figure 3c). This suggests that the physiological traits gradually increase with the growth of PH, which corresponds with the findings of Mohamed et al. (2020) and Zou et al. (2024). Because PH plays a crucial role in morphogenesis and grain yield, understanding the relationship between different traits and PH is critical for researchers to study related traits more effectively (Yu et al., 2020).

For yield-related traits, we found a positive correlation between %FG and harvest index (Figure 3d). It is known that rice grain yield is a function of HI and biomass, and that increasing either of these traits can increase grain yield. It is worth noting that HI is the parameter of conversion efficiency of DM production, and its value reflects resource use efficiency such as water and nutrient use efficiencies (Yang and Zhang, 2023).

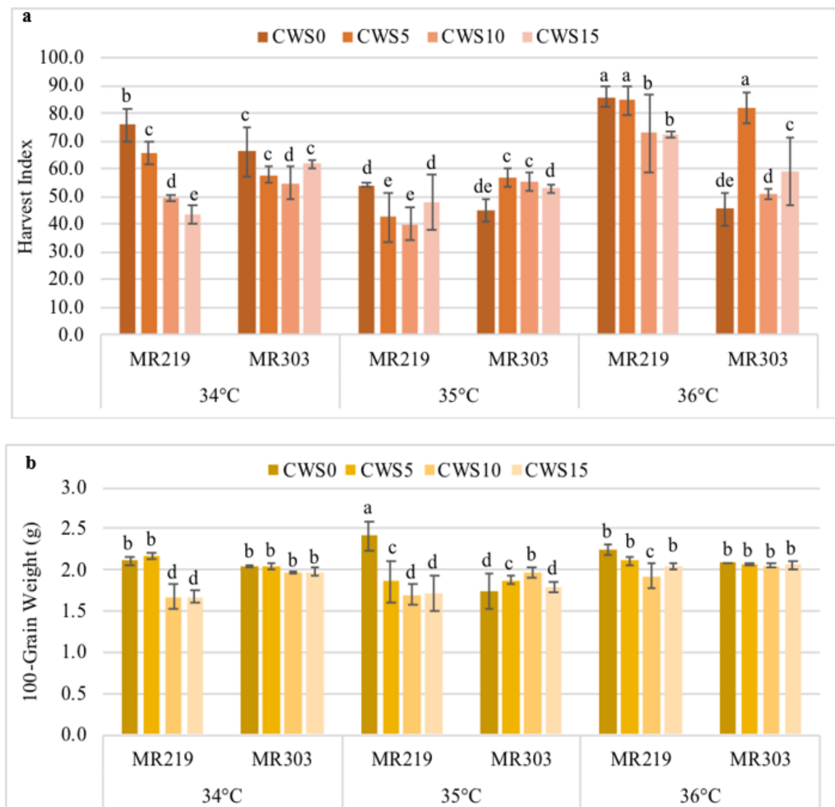

Figure 2. Effect of different cyclic water stress conditions across all three temperature settings on harvest index (HI) (a) and 100-grain weight (GW) (b) of 'MR219' and 'MR303' rices. CWS0: No cyclic water stress; CWS5: cyclic water stress for 5 d; CWS10: cyclic water stress for 10 d; CWS15: cyclic water stress for 15 d. Mean ± standard error mean (n = 3). Different letters indicate a significant difference according to Duncan's test with alpha = 0.05.

Table 3. Pearson's correlation coefficient between the measured parameters. *Significant at 5% level; **significant at 1% level; veg: vegetative; rep: reproductive; rip: ripening; PH: plant height: LAI: leaf area index; SPAD value: in-situ chlorophyll content; g_S: stomatal conductance, Chl A: chlorophyll *a* content; Chl B: chlorophyll *b* content Car: carotenoid content; HI: harvest index; %FG: fill grain percentage; GW: 100 grain weight; GtoLAI: grain to LAI ratio.

	PH -veg	PH - rep	PH - rip	LAI	SPAD Value	g_S	Chl A	Chl B	Car	HI	% FG	GW	GtoLAI
PH -veg	1												
PH - rep	0.759**	1											
PH - rip	0.736**	0.927**	1										
LAI	0.513**	0.665**	0.798**	1									
SPAD value	0.516**	0.678**	0.715**	0.597**	1								
Gs	0.362**	0.657**	0.678**	0.544**	0.458**	1							
Chl A	0.252*	0.427**	0.467**	0.324**	0.320**	0.307**	1						
Chl B	0.470**	0.574**	0.450**	0.172	0.324**	0.434**	0.174	1					
Car	-0.390**	-0.392**	-0.241*	0.002	-0.218	-0.288*	0.173	-0.888**	1				
HI	0.424**	0.180	0.105	0.126	0.009	-0.057	0.175	0.285*	-0.274*	1			
% FG	0.159	-0.201	-0.188	-0.077	-0.201	-0.380**	-0.095	-0.033	-0.016	0.630**	1		
GW	0.492**	0.339**	0.195	0.160	0.117	-0.001	0.147	0.316**	-0.286*	0.613**	0.369**	1	
GtoLAI	0.024	-0.013	-0.069	-0.348**	0.055	0.017	-0.052	0.284*	-0.353**	0.063	-0.059	-0.117	1

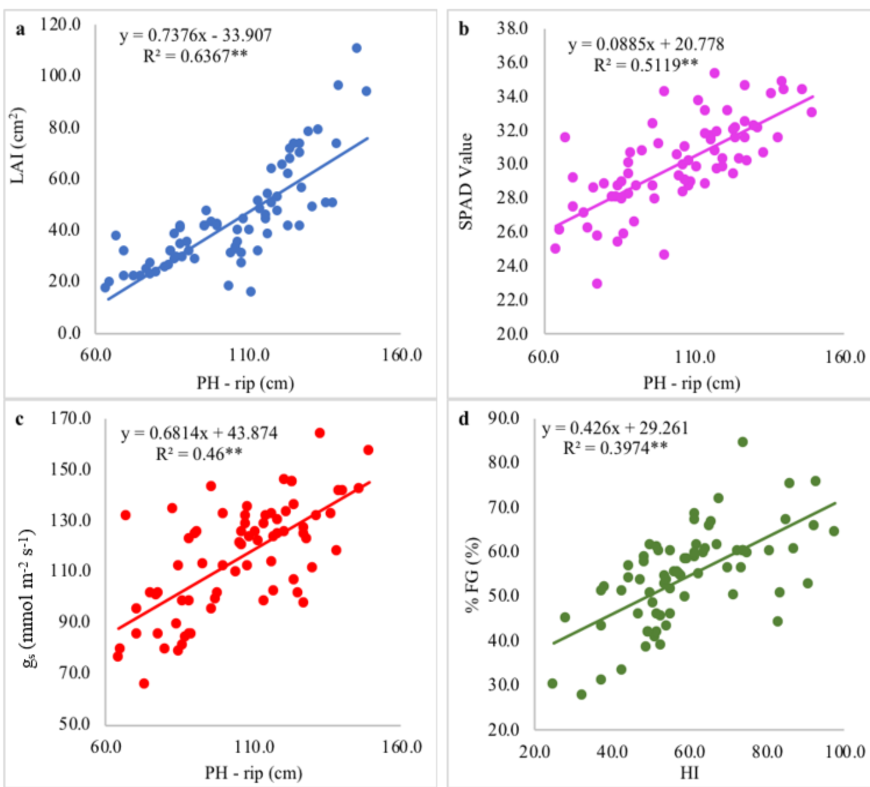

Figure 3. Linear regression analysis. The solid lines depict the regression between plant height at ripening stage (PH rip) and leaf area index (LAI) (a); PH rip and SPAD value (b); PH rip and stomatal conductance (g_S) (c); and filled grain percentage (%FG) and harvest index (HI) (d). Regression equations and correlation coefficients (R^2) are included in the plots. N = 72. **Significant at 1% level.

CONCLUSIONS

It is critical to understand how heat and drought stress, both individually and in combination, impact rice development and production, particularly for nations like Malaysia where rice production is continuously impacted by multiple climatic factors. Our findings revealed that individual heat stress had a significant impact on rice growth and yield, whereas individual drought stress mostly affected yield rather than morpho-physiology. Conversely, the combination of heat and drought stresses generally had little to nonsignificant effect on morphology and yield, but some physiological responses were affected significantly. This study also found positive correlations between several tested parameters, including harvest index and percentage of filled grain, and a better understanding of these relationships will allow rice researchers to study related traits more effectively in the future. The overall outcome of this study corresponded with part of our hypothesis that individual and combined heat and drought stress have different effects on rice development and production. However, combined stresses did not negatively impact rice production as hypothesized. We concluded that Malaysian rice cultivars respond differently to individual and combined heat and drought stress, and the findings from this study will establish a groundwork for the sustainable development of commercial local cultivars under various climatic stressors.

Author contribution

Conceptualization: A.C., N.A.M.Z. Methodology: N.A.M.Z., N.O., M.S.M. Formal analysis: G.S. Investigation: G.S, N.M.H. Resources: A.C., N.O., M.R.I. Data curation: N.A.M.Z. Writing-original draft: A.C., G.S. Writing & editing: N.A.M.Z., N.O., M.R.I., M.S.M., N.M.H. Supervision: A.C., N.A.M.Z. Project administration: A.C. Funding acquisition: A.C. All co-authors reviewed the final version and approved the manuscript before submission.

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References

Anwarmalik, M.F., Ashraf, M., Qureshi, A.S., Ghafoor, A. 2007. Assessment of genetic variability, correlation and path analyses for yield and its components in soybean. Pakistan Journal of Botany 39:405-413.

Carins-Murphy, M.R., Cochard, H., Deans, R.M., Gracie, A.J., Brodribb, T.J. 2023. Combined heat and water stress leads to local xylem failure and tissue damage in pyrethrum flowers. Plant Physiology 193(1):356-370. doi:10.1093/plphys/kiad349.

Chaudhary, A., Venkatramanan, V., Kumar Mishra, A., Sharma, S. 2023. Agronomic and environmental determinants of direct seeded rice in South Asia. Circular Economy and Sustainability 3:253-290. doi:10.1007/s43615-022-00173-x.

Das, K.R., Zaman, F., Islam, M.M., Siddiqui, S., Alshaharni, M.O., Algopishi, U.B. 2024. Physiological responses and yield performance of selected rice (*Oryza sativa* L.) genotypes under deficit moisture stress. Saudi Journal of Biological Sciences 31(4):103961. doi:10.1016/j.sjbs.2024.103961.

Dorairaj, D., Govender, N.T. 2023. Rice and paddy industry in Malaysia: Governance and policies, research trends, technology adoption and resilience. Frontiers in Sustainable Food Systems 7:1093605. doi:10.3389/fsufs.2023.1093605.

Evamoni, F.Z., Nulit, R., Yap, C.K., Ibrahim, M.H., Sidek, N. 2023. Assessment of germination performance and early seedling growth of Malaysian *indica* rice genotypes under drought conditions for strategic cropping during water scarcity. Chilean Journal of Agricultural Research 83:281-292. doi:10.4067/S0718-58392023000300281.

Heredia, M.C., Kant, J., Prodhan, M.A, Dixit, S., Wissuwa, M. 2022. Breeding rice for a changing climate by improving adaptations to water saving technologies. Theoretical and Applied Genetics 135:17-33. doi:10.1007/s00122-021-03899-8.

Kumari, A., Lakshmi, G.A., Krishna, G.K., Patni, B., Prakash, S., Bhattacharyya, M., et al. 2022. Climate change and its impact on crops: A comprehensive investigation for sustainable agriculture. Agronomy 12:3008. doi:10.3390/agronomy12123008.

Lin, W., Guo, X., Pan, X., Li, Z. 2018. Chlorophyll composition, chlorophyll fluorescence, and grain yield change in *esl* mutant rice. International Journal of Molecular Sciences 19(10):2945. doi:10.3390/ijms19102945.

Liu, H., Able, A.J., Able, J.A. 2019. Genotypic performance of Australian durum under single and combined water-deficit and heat stress during reproduction. Scientific Reports 9:14986. doi:10.1038/s41598-019-49871-x.

Mohamed, I.A.A., Shalby, N., Bai, C., Qin, M., Agami, R.A., Jie, K., et al. 2020. stomatal and photosynthetic traits are associated with investigating sodium chloride tolerance of *Brassica napus* L. cultivars. Plants 9:62. doi:10.3390/plants9010062.

Mohd Hanafiah, N., Mispan, M.S., Lim, P.E., Baisakh, N., Cheng, A. 2020. The 21st century agriculture: When rice research draws attention to climate variability and how weedy rice and underutilized grains come in handy. Plants 9:365. doi:10.3390/plants9030365.

Nugroho, A.D., Prasada, I.Y., Lakner, Z. 2023. Comparing the effect of climate change on agricultural competitiveness in developing and developed countries. Journal of Cleaner Production 406:137139. doi:10.1016/j.jclepro.2023.137139.

Oladosu, Y., Rafii, M.Y., Arolu, F., Chukwu, S.C., Muhammad, I., Kareem, I., et al. 2020. Submergence tolerance in rice: Review of mechanism, breeding and, future prospects. Sustainability 12:1632.

Ramegowda, V., Senthil, A., Senthil-Kumar, M. 2024. Stress combinations and their interactions in crop plants. Plant Physiology Reports 29:1-5. doi:10.1007/s40502-024-00785-5.

Ren, H., Bao, J., Gao, Z., Sun, D., Zheng, S., Bai, J. 2023. How rice adapts to high temperatures. Frontiers in Plant Science 14:1137923. doi:10.3389/fpls.2023.1137923.

Sehgal, A., Sita, K., Siddique, K.H.M., Kumar, R., Bhogireddy, S., Varshney, R.K., et al. 2018. Drought or/and heat-stress effects on seed filling in food crops: Impacts on functional biochemistry, seed yields, and nutritional quality. Frontiers in Plant Science 9:1705. doi:10.3389/fpls.2018.01705.

Shrestha, S., Mahat, J., Shrestha, J., Madhav K.C., Paudel, K. 2022. Influence of high-temperature stress on rice growth and development: A review. Heliyon 8(12):e12651. doi:10.1016/j.heliyon.2022.e12651.

Swapna, S., Shylaraj, K.S. 2017. Screening for osmotic stress responses in rice varieties under drought condition. Rice Science 24(5):253-263. doi:10.1016/j.rsci.2017.04.004.

Thuy, T.L., Thach, T.N., Xa, T.T.T., Nha, C.T., My, V.T.T., Nguyen, N.T.T., et al. 2021. Heat stress affects seed set and grain quality of Vietnamese rice cultivars during heading and grain filling period. Journal of Tropical Crop Science 8(3):154-160. doi:10.29244/jtcs.8.03.154-160.

Wang, B., Cai, W., Li, J., Wan, Y., Li, Y., Guo, C., et al. 2020. Leaf photosynthesis and stomatal conductance acclimate to elevated [CO_2] and temperature thus increasing dry matter productivity in a double rice cropping system. Field Crops Research 248:107735. doi:10.1016/j.fcr.2020.107735.

Williams, E., Funk, C., Peterson, P., Tuholske, C. 2024. High resolution climate change observations and projections for the evaluation of heat-related extremes. Scientific Data 11:261. doi:10.1038/s41597-024-03074-w.

Xu, Y., Chu, C., Yao, S. 2021. The impact of high-temperature stress on rice: Challenges and solutions. The Crop Journal 9(5):963-976. doi:10.1016/j.cj.2021.02.011.

Xu, X., Fonseca de Lima, C.F., Vu, L.D., De Smet, I. 2023. When drought meets heat - a plant omics perspective. Frontiers in Plant Science 14:1250878. doi:10.3389/fpls.2023.1250878.

Yadav, C., Bahuguna, R.N., Dhankher, O.P., Singla-Pareek, S.L., Pareek, A. 2022. Physiological and molecular signatures reveal differential response of rice genotypes to drought and drought combination with heat and salinity stress. Physiology and Molecular Biology of Plants 28(4):899-910. doi:10.1007/s12298-022-01162-y.

Yang, J., Zhang, J. 2023. Simultaneously improving grain yield and water and nutrient use efficiencies by enhancing the harvest index in rice. Crop and Environment 2(3):157-164. doi:10.1016/j.crope.2023.07.001.

Yousaf, M.I., Riaz, M.W., Jiang, Y., Yasir, M., Aslam, M.Z., Hussain, S., et al. 2022. Concurrent effects of drought and heat stresses on physio-chemical attributes, antioxidant status and kernel quality traits in maize (*Zea mays* L.) hybrids. Frontiers in Plant Science 11(13):898823. doi:10.3389/fpls.2022.898823.

Yu, W., Ji, R., Wu, J., Feng, R., Mi, N., Chen, N. 2023. Combined effects of heat and drought stress on the growth process and yield of maize (*Zea mays* L.) in Liaoning Province, China. Atmosphere 14:1397. doi:10.3390/atmos14091397.

Yu, M., Liu, ZH., Yang, B., Chen, H., Zhang, H., Hou, D.B. 2020. The contribution of photosynthesis traits and plant height components to plant height in wheat at the individual quantitative trait locus level. Scientific Reports 10:12261. doi:10.1038/s41598-020-69138-0.

Zain, N.A., Ismail, M.R., Mahmood, M., Puteh, A., Ibrahim, M.H. 2014. Alleviation of water stress effects on MR220 rice by application of periodical water stress and potassium fertilization. Molecules 19(2):1795-819. doi:10.3390/molecules19021795.

Zainol, R.M., Ashri, N.A, Mohd Rosmi, M.N., Ibrahim, M.S.N. 2023. The effect of using quality rice seed varieties on rice cultivation activities. Journal of Food Technology Research, Conscientia Beam 10(3):62-74.

Zhang, Q., Akhtar, R., Mohammad Saif, A.N., Akhter, H., Hossan, D., Alam, A., et al. 2023. The symmetric and asymmetric effects of climate change on rice productivity in Malaysia. Heliyon 9(5):e16118. doi:10.1016/j.heliyon.2023.e16118.

Zou, M., Liu, Y., Fu, M., Li, C., Zhou, Z., Meng, H., et al. 2024. Combining spectral and texture feature of UAV image with plant height to improve LAI estimation of winter wheat at jointing stage. Frontiers in Plant Science 14:1272049. doi:10.3389/fpls.2023.1272049.

Zuki, Z.M., Rafii, M.Y., Ramli, A., Oladosu, Y., Latif, M.A., Sijam, K., et al. 2020. Segregation analysis for bacterial leaf blight disease resistance genes in rice using SSR marker. Chilean Journal of Agricultural Research 80:227-233. doi:10.4067/S0718-58392020000200227.