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Effect of High Temperature on Growth and Yield of Lettuce

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ABSTRACT

It is predicted that the average world temperature will rise by 1.5 ºC in the next few decades, which may adversely affect vegetable productivity and global food security. The present study aimed to identify lettuce genotype(s) that are tolerant of heat stress so that they may be good candidates for future breeding programs to develop heat-stress-tolerant lettuce cultivars. While using a complete randomized design with three replicates, we evaluated the performance of eight lettuce genotypes using a hydroponic system under non-stress (controlled) and heat stress (high temperature) environmental treatments. The effects of environmental treatments on the morpho-physiological and agronomic characteristics of the genotypes were assessed. Ten traits were recorded after harvest, i.e., the number of leaves, plant height, root length, yield, fresh root weight, plant weight, leaf area, leaf width, leaf length, and chlorophyll contents. In general, lettuce genotypes cultivated under heat stress exhibited decreased performance in most traits compared to the non-stress treatment group. The yield of SAL092, SAL093, SAL094, SAL095, SAL096, SAL097, and SAL099 decreased by 65.8%, 66.4%, 65%, 28.2%, 40.6%, 76.3%, and 73.1%, respectively, under heat stress. In contrast, SAL098 grown under non-stress conditions showed higher yield, leaf count, root length, plant weight, and plant height by 0.1%, 15.2%, 0.9%, 4%, and 27%, respectively, compared to non-stress conditions. In addition, during heat stress, every trait exhibited a positive correlation with yield, except leaf width, suggesting that productive attributes are crucial for enhancing yield under high-temperature conditions. SAL095 and SAL098 exhibited effective adaptive mechanisms and may be regarded as potential heat-tolerant genotypes for future breeding programs and developing heat-tolerant cultivars and high yields.

Abbreviation: Chlorophyll Content (CC), Fresh Root Weight (FRW), Heat stress (HS), Leaf Area (LA), Leaf Length (LL), Number of leaves per plant (LN), Leaf Width (LW), Non- stress (NS), Plant height (PH), Plant Weight (PW), Root length (RL), Yield (YLD)

Introduction

The projected rise in global population to around 8.9 billion people by 2050 will necessitate a 50% increase in food production worldwide (Mir et al., 2022). Currently, almost 55% of the world's population lives in urban regions or cities

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(Saharan and Choudhary, 2022). However, it is projected that by 2050, the urban population will increase to 6-9 billion as a result of significant migration to urban areas (Chatterjee et al., 2022). Therefore, it is essential to improve the food industries in urban areas to satisfy the increasing dietary needs of the fast-growing urban population. Regrettably, relying on traditional or soil-based farming methods in these areas to provide sustenance for the urban population is difficult due to the decreasing availability of fertile land with the exorbitant cost of the restricted land in urban areas. In addition to the problems mentioned earlier, traditional farming faces various other challenges such as soil infertility and degradation, erosion, extreme climate events like salinity, drought, flooding, temperate stress, pollution, and depleted soil nutrients leading to low yield and productivity (Chatterjee et al., 2022; Gumisiriza et al., 2022; Gumisiriza et al., 2023). Moreover, the cost of transporting food commodities from the production site to urban areas is considerably high and can make certain commodities unsellable due to factors such as pathogen infestation. This issue necessitates resolution to ensure that all individuals in urban areas can obtain fresh, nutritious, and superior-quality food. Urban farming is a practical and environmentally friendly solution to address the rising food needs of urban populations (Saharan and Choudhary, 2022).

Urban farming refers to practicing crop cultivation in empty or small land areas located within or near urban areas. The resulting products are meant, at least in part, for consumption by urban residents (Gumisiriza et al., 2023). The resilience of this farming production system is greater compared to traditional agricultural systems, primarily because it has a shorter supply chain for urban populations and involves a wider range of farming operations. Urban farming systems have a crucial role in improving food security and sustainability, enhancing production systems, boosting a country's economic position, and providing easy access to fresh produce for urban residents (Gumisiriza et al., 2023). According to Payen et al. (2022), approximately 15% and 20% of the world's food production takes place in urban and peri-urban areas. The hydroponic system is a gardening technology commonly used in urban farming. This method utilizes a nutrient solution to cultivate diverse crops, particularly vegetables such as lettuce, spinach, cucumbers, and tomatoes. The hydroponic technique necessitates a minimal quantity of water for production in contrast to conventional farming methods, as well as a shorter period of growth (Gumisiriza et al., 2022). This innovation has fulfilled the expectations of urban farmers by increasing crop productivity and shortening the production cycle, thus improving food security and accessibility.

The temperature range of 15~20 °C is optimal for lettuce growth (He et al., 2022). While the implementation of hydroponic systems in urban areas has enhanced crop yield, the occurrence of severe weather conditions, such as high temperatures, remains an important issue. This adversely impacts growth, productivity, and crop marketability, particularly lettuce, and poses challenges for urban farmers, particularly those with limited financial resources who cannot afford costly infrastructure to create an optimal growth environment. High temperatures in crops have detrimental effects on their functionality, leading to the formation of reactive oxygen species (ROS) within plant cells. This, in turn, causes peroxidation of membrane pigments and a loss of membrane permeability (dos Santos et al., 2022; Oyebamiji et al., 2023). Moreover, high temperature induces unusual alterations in cellular structure as a result of plant cell injury or mortality (Yu et al., 2022). Heat stress induces a significant decrease in plant growth, development, and overall productivity (Srivastava et al., 2022). A recent study by Wang et al. (2023) reported that reductions occurred in growth traits, gas exchange parameters, and photosystem function of water spinach at 45 °C. At temperatures exceeding 30 °C, canola seed yield decreased by 89% (Hasanuzzaman et al., 2013). Over the next few decades, there is an anticipated increase in the global average temperature by 1.5 ºC, thus directly affecting lettuce production and global food security, particularly in urban areas. Previous research has been rare on the performance of lettuce cultivated in hydroponic systems under heat-stress conditions. Thus, the primary objective of this study was to identify lettuce genotypes that demonstrate higher heat tolerance and consistent performance in dealing with the effects of high temperatures, making them suitable for cultivation in urban areas and potentially contributing to future heat stress tolerance breeding initiatives for lettuce.

Materials and Methods

Study site and plant materials

The study was conducted in the growth chamber of the Plant Biotechnology Laboratory and Greenhouse 4 of the Greenhouse Complex at Universiti Kebangsaan Malaysia in Bangi, Selangor. For instance, Selangor, Malaysia the temperature fluctuates between 22.8 °C and 31.9 °C, while the yearly rainfall varies from 48 mm to 150 mm. This study utilized eight lettuce genotypes, namely SAL092, SAL093, SAL094, SAL095, SAL096, SAL097, SAL098, and SAL099 (Table 1). All of these genotypes were obtained from the World Vegetable Centre in Taiwan, except SAL098, which was purchased from a local market. The genotypes (except for SAL098) were recommended by the World Vegetable Centre.

Table 1. List of lettuce genotypes.

Code	Name/Identification Number	Source
SAL092	VI050276	World Vegetable Center
SAL093	VI046273	World Vegetable Center
SAL094	VI047362	World Vegetable Center
SAL095	VI050271	World Vegetable Center
SAL096	VI050217	World Vegetable Center
SAL097	VI049278	World Vegetable Center
SAL098	Red oakleaf lettuce	Commercial Store
SAL099	VI047533	World Vegetable Center

Growth conditions, experimental design and data collection

All genotypes were screened under controlled non-stress (NS) and heat-stress (HS) environmental treatments. They were grown using a basic non-circulating hydroponic system (stagnant nutrient solution) as part of the experimental protocol. The lettuce seedlings of each genotype germinated in the growth chamber at the Plant Biotechnology Laboratory. The temperature was 22 °C, the humidity was 60–70%, and the light cycle was 16 h/8 h of photoperiod. The current study was conducted from October to December 2021. Three-week-old seedlings were placed in hydroponic systems (15 cm x 15 cm) under NS and HS conditions, using a randomized complete design (CRD) with three replicates. Before placing the plant into the systems, seedling roots were gently cleaned to remove peat particles. Then, the bare roots were immersed in a stagnant nutrient solution. The composition of the AB nutrient solution utilized is listed in Table 2. The nutrient solution was refilled when it diminished as a result of being absorbed by the plant. The nutrition solution pH was closely monitored and maintained between 5.5 and 6.5 by adding hydrochloric acid and sodium hydroxide, by the conditions at the time. The experiment was conducted in a controlled environment where the temperature and relative humidity were consistently maintained at 22 °C and 60-70%, respectively. The temperature and relative humidity in the heat-stress treatment were measured three times daily (Morning: 8:00 AM – 10:00 AM, Afternoon: 12:00 PM – 2:00 PM, and Evening: 5:00 PM – 7:00 PM) using a thermo-hygrometer throughout the experiment (Table 3). Fifty days after germination, the plants were harvested to gather the following data:

Number of leaves per plant (LN): leaf count at harvest was determined per plant.
Plant height (PH): plant height was measured in cm using a measuring tape from the basal point to the plant apex.
Root length (RL): root length was measured in cm using a measuring tape from the shoot base to the apex of the root for each replicate.
Leaf Area (LA): the area covered by each leaf was measured by placing the leaf for each replicate on a graph sheet, and the leaf contour was traced with a pencil. Then, each square inside the contour was counted and added up.
Leaf Length (LL): leaf length was measured in cm from the end of the petiole to the tip of the terminal leaflet using a measuring tape.
Leaf Width (LW): leaf width was measured in cm from the widest point of the leaf to the other using a measuring tape.
Chlorophyll Content (CC) (SPAD value): total chlorophyll contents produced in the leaves were determined using a digital chlorophyll meter (SPAD meter).
Plant Fresh Weight (PFW): plant fresh weight was measured in g using a digital weighing balance.
Yield (YLD): yield was determined in g by weighing the whole plant excluding the roots using a digital weighing balance.
Root Fresh Weight (RFW): root fresh weight was measured in g using a digital weighing balance.

Table 2. Chemical contents of nutrient solution (mg L^{-1}).

Element	Concentration (%)
Set A	
Nitrogen	15.5
CaO	26
Set B	
NO_3	3
P_2O_5	10
K_2O	30
MgO	8
SO_3	28
B	0.022
Cu-EDTA	0.004
Fe-EDTA	0.06
Fe-DTPA	0.08
Mn-EDTA	0.033
Mo	0.003
Zn-EDTA	0.02

Table 3. Mean of Air Temperature and Relative Humidity of the Greenhouse of Heat-Stress Treatment.

Trial	Morning Temperature (°C)	Afternoon Temperature (°C)	Evening Temperature (°C)	Morning Relative Humidity (%)	Afternoon Relative Humidity (%)	Evening Humidity (%)
Heat Stress Treatment	25.1 – 30.0	25.0 – 40.8	25.1 – 32.8	69.6 – 87.6	43.8 – 90.1	57.6 – 93.3
Mean	27.5	34.1	29.2	80.3	58.6	74.6
Total Mean		30.3			71.1	

Statistical analysis

The analyses of variance (ANOVA) were performed on all of the data. To assess the statistical differences between the means of the lettuce genotypes under the two environment treatments, a t-test was performed using Minitab version 15. In addition, RStudio version 1.2.5003 was utilized to conduct the Tukey (HSD) test to determine whether there were statistically significant differences between the mean values of genotypes screened under NS and HS treatments for every trait. For each environmental treatment, Pearson's correlation coefficients between traits were determined and displayed using the ggplot in RStudio version 1.2.5003.

Results

Phenotypic analysis

Table 4 shows summarized descriptive statistics of all evaluated morpho-physiological and agronomical traits under environmental treatments using the mean and coefficient of variance as indicators. The mean ranges from 0.37 to 90.96 for non-stress (NS) and heat stress (HS) treatments. The minimum and maximum mean under both treatments were recorded for PDW (NS = 0.82, HS = 0.37) and LA (NS = 90.96 and HS = 50.33) respectively. Six traits (LN, PH, RL, LL, LW, and LA) and three traits (LN, PH, and RL) under HS and NS recorded low CV (< 30%). All other traits have a moderate to high CV under both treatments with FRW (NS = 97, HS = 105) possessing the highest CV (> 90).

The analysis of variance (ANOVA) showed significant differences in all traits for treatment, genotype, and treatment × genotype. Concerning the treatment, all traits showed significant differences except the root length (RL) and leaf length (LL), while for genotype, all traits showed significant differences. Apart from leaf number (LN) and chlorophyll content (CC) of treatment × genotype, all other traits were significantly different (Table 5). Table 6 shows the t-test results, which indicated significant differences between the traits under both environmental treatments. This showed the effect of environmental factors on the morpho-physiological traits of the genotypes in the two conditions. A significant difference was observed in non-stress (NS) and heat stress (HS) for all studied traits.

Table 4. Descriptive statistics for all traits.

Traits	Min		Max		Mean ± SE		CV (%)	
	NS	HS	NS	HS	NS	HS	NS	HS
LN	6.00	6.00	16.00	14.00	10.98 ± 0.53	10.33 ± 0.42	23	20
PH	16.00	21.20	42.00	51.60	27.26 ± 1.41	33.70 ± 1.54	25	22
RL	17.30	15.50	37.70	27.50	23.06 ± 1.03	21.13 ± 0.76	22	18
YLD	4.30	1.25	40.56	18.49	13.18 ± 1.77	6.09 ± 0.96	66	78
FRW	0.62	0.10	13.26	2.75	3.14 ± 0.62	0.67 ± 0.14	97	105
PW	0.32	0.10	1.76	1.02	0.82 ± 0.10	0.37 ± 0.06	60	80
LA	19.00	7.50	45.00	29.00	27.65 ± 6.82	17.00 ± 1.38	25	40
LW	5.10	3.80	12.00	21.20	7.91 ± 0.35	9.04 ± 1.08	21	59
LL	13.30	12.40	32.00	36.40	20.66 ± 1.11	20.04 ± 1.56	26	38
CC	13.10	10.00	43.40	32.70	24.61 ± 1.80	19.05 ± 1.15	36	30

LN = Number of leaves per plant, PH = PH = Plant height in cm, RL = Root length in cm, YLD = Yield per plant in gram, FRW = Fresh root weight in gram, PW = Plant weight in gram, LA = Leaf area in cm^2, LW = leaf width in cm, LL = leaf Length in cm, CC = Chlorophyll Contents, CV = Coefficient of variation (%), SE = Standard error, NS = Non-stress condition, HS = Heat stress condition.

Table 7 presents the comparison of morphological and physiological traits of lettuce genotypes under heat stress and non-stress conditions. Generally, the morpho-physiological traits of the genotypes were reduced under heat stress (HS) conditions compared to non-stress (NS) conditions, while plant height (PH) was increased under (HS) conditions. Concerning leaf count (LN), the occurrence of warm daytime temperatures did not cause a univocal response among the genotypes. However, a reduction in the LN by 7.4%, 10%, 1.8%, 21.1%, and 23.1% was observed in SAL092, SAL094, SAL096, SAL097, and SAL099 respectively under HS conditions. In contrast, an increase in the LN of SAL093, SAL095, and SAL098 by 4.4%, 4.7%, and 15.2%, respectively, was recorded under HS conditions.

Genotypes grown under HS conditions were taller compared to the control except SAL096, which recorded a 3.5% reduction. The highest increase in PH was observed in SAL092, with 44.5% under the HS trial compared to NS conditions (Table 7).

For root length (RL), five genotypes, i.e., SAL092, SAL093, SAL094, SAL096, and SAL097 under the NS condition had higher mean values compared to HS. However, three genotypes, i.e., SAL095, SAL098, and SAL099 under the HS recorded higher mean values than control genotypes. The mean values of all genotypes were not significantly different, except for SAL095 (NS = 20.00, HS = 26.23), which was significantly different. Concerning yield (YLD), warm daytime temperatures caused a univocal response among the genotypes screened. A reduction in the yield by 65.8%, 66.4%, 65%, 28.2%, 40.6%, 76.3% and 73.1% was observed in SAL092, SAL093, SAL094, SAL095, SAL096, SAL097, and SAL099, respectively, under HS conditions. In contrast, an increase in the YLD of SAL098 by 0.1% was recorded under HS conditions compared to NS.

Table 5. Analysis of variance of all traits.

SOV	Df	LN	PH	RL	YLD	FRW	PW	LA	LW	LL	CC
Treatment	1	5.00*	496.33**	44.56	603.29**	73.45**	1077.49**	1360.00***	15.53**	4.59	371.58**
Error (a)	4	0.27	8.07	24.44	15.82	1.29	25.63	11.47	0.36	1.18	8.97
Genotype	7	22.68***	247.36***	28.68**	185.14***	15.93***	302.02***	108.05***	39.29***	256.19***	292.28***
Treatment × Genotypes	7	4.02	50.79**	48.85***	47.39*	7.63**	87.73*	118.58***	45.16***	19.29***	23.24
Error (b)	28	2.22	10.39	9.69	19.90	1.92	32.91	17.69	4.29	3.62	9.92
Total	47										

LN = Number of leaves per plant, PH = Plant height in cm, RL = Root length in cm, YLD = Yield per plant in gram, FRW = Fresh root weight in gram, PW = Plant weight in gram, LA = Leaf area in cm^2, LW = leaf width in cm, LL = leaf Length in cm, CC = Chlorophyll Contents *p < 0.05, **p < 0.01, ***p < 0.001.

Table 6. Mean comparison for treatment × genotype under heat-stress and non-stress treatments.

Genotype	Treatment	LN	PH	RL	YLD	FRW	PW	LA	LW	LL	CC
SAL092	HS	10.33^{a}	34.17^{a}	18.28^{a}	4.45^{a}	0.27^{a}	4.87^{a}	12.67^{a}	15.07^{a}	14.45^{a}	27.87^{a}
	NS	11.17^{a}	18.97^{b}	30.43^{a}	13.03^{b}	0.78^{b}	13.81^{b}	23.83^{b}	8.25^{b}	15.85^{b}	40.40^{b}
SAL093	HS	8.33^{a}	26.93^{a}	18.60^{a}	2.18^{a}	0.20^{a}	2.37^{a}	12.33^{a}	15.60^{a}	13.97^{a}	14.57^{a}
	NS	8.00^{a}	25.75^{a}	21.43^{b}	6.46^{b}	0.78^{b}	7.25^{b}	26.67^{b}	7.63^{a}	17.62^{b}	21.22^{a}
SAL094	HS	11.67^{a}	30.67^{a}	24.83^{a}	3.28^{a}	0.21^{a}	3.48^{a}	8.50^{a}	4.33^{a}	13.90^{a}	14.73^{a}
	NS	13.00^{a}	24.57^{a}	25.27^{a}	9.38^{a}	3.04^{b}	12.42^{b}	23.67^{b}	8.50^{b}	17.37^{b}	17.97^{b}
SAL095	HS	12.83^{a}	48.00^{a}	26.23^{a}	16.77^{a}	2.22^{a}	18.97^{a}	23.83^{a}	4.60^{a}	34.53^{a}	23.53^{a}
	NS	12.17^{a}	35.13^{b}	20.00^{a}	23.42^{a}	7.62^{a}	31.00^{a}	31.00^{a}	7.00^{b}	27.60^{b}	31.00^{a}
SAL096	HS	9.33^{a}	30.00^{a}	16.60^{a}	4.30^{a}	0.54^{a}	4.84^{a}	21.17^{a}	4.33^{a}	24.33^{a}	21.60^{a}
	NS	9.50^{a}	31.13^{a}	20.33^{b}	7.24^{b}	1.77^{b}	9.02b	22.17^{a}	5.90^{b}	23.03^{a}	24.80^{a}
SAL097	HS	7.50^{a}	35.73^{a}	19.53^{a}	2.91^{a}	1.57a	2.62^{a}	10.67^{a}	5.30^{a}	14.73^{a}	14.93^{a}
	NS	9.50^{a}	26.67^{b}	25.67^{a}	12.27^{b}	2.37^{b}	14.64^{b}	37.50^{b}	10.77^{b}	18.17^{b}	15.87^{a}
SAL098	HS	11.00^{a}	25.57^{a}	21.33^{a}	7.94^{a}	0.94^{a}	10.04^{a}	24.50^{a}	9.30^{a}	16.60^{a}	13.50^{a}
	NS	9.33^{a}	18.67^{a}	21.07^{a}	7.93^{a}	1.65^{a}	9.60^{a}	22.83^{a}	8.83^{a}	15.90^{a}	15.40^{b}
SAL099	HS	11.67^{a}	38.50^{a}	23.62^{a}	6.92^{a}	0.79^{a}	7.61^{a}	22.33^{a}	13.82^{a}	27.80^{a}	21.63^{a}
	NS	15.17^{b}	37.23^{a}	20.25^{a}	25.72^{b}	7.11^{b}	32.84^{b}	33.50^{b}	6.37^{b}	29.73^{a}	30.23^{b}

LN = Number of leaves per plant, PH = Plant height in cm, RL = Root length in cm, YLD = Yield per plant in gram, FRW = Fresh root weight in gram, PW = Plant weight in gram, LA = Leaf area in cm^2, LW = leaf width in cm, LL = leaf Length in cm, CC = Chlorophyll contents, NS = Non-stress condition, HS = Heat stress conditions. Mean values for each genotype with the same letter under HS and NS are not significantly different according to the t-test ($P<0.05$).

The fresh root weight (FRW) of all genotypes in HS was reduced compared to the NS condition, while the reduction in the FRW was significant in all genotypes under NS and HS conditions, except SAL095 and SAL099. The highest mean value in the NS condition was recorded for SAL095 (7.62), while the lowest under the same condition was in SAL092 and SAL093 (0.78). Meanwhile, the highest and the lowest mean value under HS were recorded for SAL095 (2.22) and SAL097 (0.16), respectively. Regarding plant weight (PW), the mean recorded for genotypes (SAL092, SAL093, SAL094, SAL095, SAL096, and SAL097) under HS was lower than the NS condition. However, SAL098 (NS = 10.04, HS = 9.60) recorded a higher mean value under the HS trial than in the NS trial. The highest and lowest values were recorded for SAL099 (32.83) and SAL093 (7.24) under the NS condition. SAL095 (19.00) and SAL093 (2.32) had the highest and lowest mean value under HS conditions. The performance of all genotypes grown under NS conditions increased, except in SAL098, which was reduced by 4% compared to the HS trial.

High-day time temperature caused a reduction in the leaf area (LA) of all genotypes compared to the NS, excluding SAL098, which increased by 6.8% under the HS trial. Similarly, the chlorophyll content of all genotypes in the HS trial was reduced compared to the NS trial. Maximum leaf width (LW) was observed in SAL092 and SAL093 under HS conditions while the lowest was obtained in SAL094 and SAL096 under similar conditions. Based on the result, three genotypes (SAL095, SAL096, and SAL098) in the HS trial have increased leaf length (LL) compared to counterparts in NS. Five genotypes (SAL092, SAL093, SAL094, SAL097, and SAL099) had higher LL in the NS trial than in the HS condition.

Table 7. Mean comparison for eight lettuce genotypes under heat-stress and non-stress treatments.

Genotype	LN		PH		RL		YLD		FRW		PW		LA		LW		LL		CC	
	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS	HS	NS
SAL092	10.33	11.17	34.17^{bc}	18.97^{d}	18.28^{ab}	30.43^{a}	4.45^{b}	13.03^{bc}	0.27^{a}	0.78^{b}	4.87^{ab}	13.81^{b}	12.67^{bcde}	23.83^{bc}	15.07^{a}	8.25^{a}	14.45^{c}	15.85^{d}	27.87	40.40
SAL093	8.33	8.00	26.93^{c}	25.75^{cd}	18.60^{ab}	21.43^{b}	2.18^{b}	6.46^{c}	0.20^{a}	0.78^{b}	2.37^{b}	7.25^{b}	12.33^{cde}	26.67^{abc}	15.60^{a}	7.63^{a}	13.97^{c}	17.62^{d}	14.57	21.22
SAL094	11.67	13.00	30.67^{bc}	24.57^{cd}	24.83^{ab}	25.27^{ab}	3.28^{b}	9.38^{c}	0.21^{a}	3.04^{b}	3.48^{b}	12.42^{b}	8.50^{e}	23.67^{bc}	4.33^{c}	8.50^{a}	13.90^{c}	17.37^{d}	14.73	17.97
SAL095	12.83	12.17	48.00^{a}	35.13^{ab}	26.23^{a}	20.00^{b}	16.77^{a}	23.42^{ab}	2.22^{a}	7.62^{a}	18.97^{a}	31.00^{a}	23.83^{ab}	31.00^{abc}	4.60^{c}	7.00^{a}	34.53^{a}	27.60^{ab}	23.53	31.00
SAL096	9.33	9.50	30.00^{bc}	31.13^{abc}	16.60^{b}	20.33^{b}	4.30^{b}	7.24^{c}	0.54^{a}	1.77^{b}	4.84^{ab}	9.02^{b}	21.17^{abcd}	22.17^{c}	4.33^{c}	5.90^{a}	24.33^{b}	23.03^{bc}	21.60	24.80
SAL097	7.50	9.00	35.73^{b}	26.67^{bcd}	19.53^{ab}	25.67^{ab}	2.91^{b}	12.27^{bc}	1.57a	2.37^{b}	2.62^{b}	14.64^{b}	10.67^{de}	37.50^{a}	5.30^{c}	10.77^{a}	14.73^{c}	18.17^{cd}	14.93	15.87
SAL098	11.00	9.33	25.57^{c}	18.67^{d}	21.33^{ab}	21.07^{b}	7.94^{ab}	7.93^{c}	0.94^{a}	1.65^{b}	10.04^{ab}	9.60^{b}	24.50^{a}	22.83^{bc}	9.30^{bc}	8.83^{a}	16.60^{c}	15.90^{d}	13.50	15.40
SAL099	11.67	15.17	38.50^{b}	37.23^{a}	23.62^{ab}	20.25^{a}	6.92^{ab}	25.72^{a}	0.79^{a}	7.11^{a}	7.61^{ab}	32.84^{a}	22.33^{abc}	33.50^{ab}	13.82^{ab}	6.37^{a}	27.80^{b}	29.73^{a}	21.63	30.23

LN = Number of leaves per plant, PH = Plant height in cm, RL = Root length in cm, YLD = Yield per plant in gram, FRW = Fresh root weight in gram, PW = Plant weight in gram, LA = Leaf area in cm^2, LW = leaf width in cm, LL = leaf length in cm, CC = Chlorophyll contents, NS = Non-stress condition, HS = Heat stress conditions. Mean values with the same letter at each column are not significantly different according to Tukey's test (HSD) ($P<0.05$).

The difference between genotypes of SAL095 under NS and HS conditions was significant. The SAL095 (34.50) and SAL094 (13.90) had the highest and lowest LL values in the HS trial.

Correlation between traits under non-stress and heat stress conditions

Figures 1a and b show a pictorial representation of Pearson's correlation coefficients between traits evaluated under NS and HS conditions. Under NS conditions, yield is positively significantly correlated with PW ($r = 0.99$ $p < 0.001$), FRW ($r = 0.90$ $p < 0.001$), LL ($r = 0.74$, $p < 0.001$), PH ($r = 0.66$ $p < 0.001$), LN ($r = 0.66$ $p < 0.01$), LA ($r = 0.37$, $p < 0.05$), but not significantly correlated with CC ($r = 0.34$, $p > 0.05$) and negatively correlated with LW ($r = -0.10$, $p > 0.05$) and RL ($r = -0.20$, $p > 0.05$). LN shows a positive and significant correlation with five traits (PW, yield, FRW, and LL) but was not significantly correlated with traits such as PH, LA, CC, RL and negatively correlated with LW ($r = -0.29$, $p > 0.05$).

Under HS conditions, YLD was found to be positively and significantly correlated with traits such as PW ($r = 0.96$, $p < 0.001$), PDW ($r = 0.94$, $p < 0.001$), FRW ($r = 0.98$, $p < 0.001$), LL ($r = 0.81$, $p < 0.001$), PH ($r = 0.69$, $p < 0.001$), LN ($r = 0.59$ $p < 0.01$), LA ($r = 0.68$, $p < 0.01$) and RL ($r = 0.57$, $p < 0.01$) but not significant with CC ($r = 0.30$, $p > 0.05$) and negatively correlated with LW ($r = -0.23$, $p > 0.05$). LN shows a positive correlation with all traits but correlated significantly with PW, PDW, FRW, YLD, RL, LL, and PH, and non-significant with other traits. LA was positively and significantly correlated with traits including FRW, YLD, PW, PDW, and LL but not significantly correlated with CC ($r = 0.14$, $p > 0.05$), RL ($r = 0.15$, $p > 0.05$), LN ($r = 0.32$, $p > 0.05$), PH ($r = 0.23$, $p > 0.05$), and negatively correlated with LW ($r = -0.07$, $p > 0.05$). LW negatively correlated with all traits except LN ($r = 0.03$, $p > 0.05$) and CC ($r = 0.17$, $p > 0.05$).

Discussion

Heat stress (HS) significantly reduces the productivity of lettuce cultivated in diverse environments, with particular emphasis on arid regions characterized by high temperatures. Urgent action is required to identify genotypes with the potential to be utilized in breeding initiatives aimed at minimizing yield loss under HS. The process of breeding for HS tolerance and prospective genotypes requires the evaluation of numerous genotypes across diverse heat regimes. We assessed the effects of fluctuating environmental temperatures on the morpho-physiological and agronomical traits of lettuce in comparison to the ideal condition in the present study. Throughout the study, the average day and evening temperature was 34.1/29.2 ºC, and the total mean temperature (30.3 ºC) (as shown in Table 3) exceeded the optimal temperature range of 17-28 ºC required for lettuce growth. This indicates that HS in the present study, at temperatures exceeding 28 ºC, can disrupt crop growth and development.

In addition, the observed high total mean relative humidity (> 70%) indicates that a potential rise in relative humidity could worsen the impacts of HS on the crop (Ayenan et al., 2022). Therefore, relative humidity and temperature should be considered when screening for genotypes with heat tolerance to define the optimal growing conditions.

The study observed that HS leads to a decrease in all traits except plant height (PH) and leaf width (LW) compared to NS. This rise in PH and LW could be attributed to the plant's capacity to mitigate the effects of stress. The increases in PH and LW are consistent with previous studies (Hinojosa et al., 2019; Zheng et al., 2020; Bhattarai et al., 2021; Srivastava et al., 2022). The yield and its components were reduced in all genotypes under HS with SAL095 and SAL096, recording the lowest yield reductions (28.39% and 40.61%). However, SAL098 exhibited a greater yield and plant weight (PW) compared to the NS treatment, but the difference was not statistically significant. A similar report was observed by Ayenan et al. (2022), confirming that vegetables are affected by HS, but their variation in performance is genotype-dependent. The decrease in yield may be associated with increased dephosphorylation, hydrogen peroxide, and reduced efficiency of photosystem II of photosynthesis and nitrate reductase in the plant (Lefsrud et al., 2005).

There were no significant differences in the LN between the NS and HS treatments for all genotypes, except for SAL099 (Table 6). Lee et al. (2022) observed that the LN of tomato genotypes cultivated under stress and optimal conditions did not exhibit significant variation. A decline in LN during HS conditions may be associated with cellular injury and gradual leaf abscission in plants (Ayenan et al., 2022).

Nevertheless, the final result is contingent upon variables such as the plant species, genetic makeup, and the magnitude and duration of the stress. A decrease in LA observed in genotypes grown in HS treatment may be due to reduced leaf growth, as a result of concurrent declines in turgor potential and water potential, as well as a decrease in cell division and expansion. This may be associated with a decrease in the active photosynthesis site and the leaf mass area, indicating the vulnerability of genotypes to HS (da Cruz Bento, 2020; Formisano et al., 2021). Lee et al. (2022) also reported a reduction in the LA of tomato plants under high temperatures (38/18 ºC and 41/18 ºC), as in the present study.

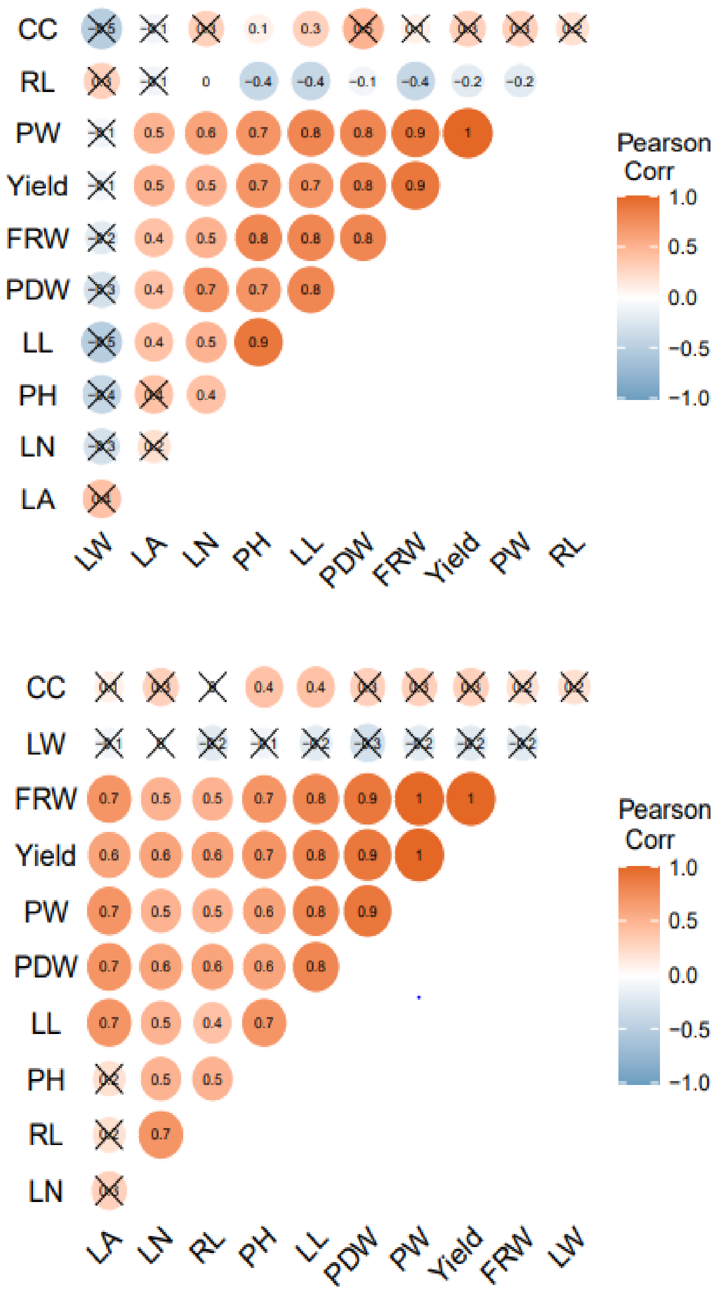

Fig. 1. Correlation matrix of traits evaluated. A = Non-stress, B = Heat stress, LN = Number of leaves per plant, PH = Plant height in cm, RL = Root length in cm, YLD = Yield per plant in gram, FRW = Fresh root weight in gram, PW = Plant weight in gram, LA = Leaf area in cm2, LW = leaf width in cm, LL = leaf length in cm, CC = Chlorophyll contents. The orange colour signifies a positive correlation while the blue signifies a negative correlation. The cross signifies no significant correlation between traits. * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$.

The root is a vital organ of the plant, facilitating the absorption and transportation of nutrients and water, as well as enabling the plant to adapt to various environmental conditions (Faiz et al., 2020). The decreased rate of root development (RL and FRW) found in this study for most of the genotypes can be related to the osmotic effect, reduced water uptake, and metabolic activities (Hussain et al., 2021). High temperatures can decrease water absorption by reducing root hydraulic conductance, increased suberization, or the deposition of secondary cell wall materials. This results in a decrease in xylem vessel diameter, which consequently increases axial resistance to water uptake. Ultimately, these factors negatively impact overall plant growth (Falah et al., 2010).

The higher daytime temperature adversely impacted the CC of the plant, potentially leading to the degradation of the photosynthetic apparatus, inhibition of photosynthetic enzymes, reduced transpiration rate due to stomatal closure, decreased leaf expansion, and initiation of senescence. Consequently, the growth of the plant is hindered (dos Santos et al., 2022). The current findings align with previous research that documented a decrease in chlorophyll levels in response to high temperatures (Faiz et al., 2020). In contrast, Bhattarai et al. (2021) reported improved CC under HS conditions, which they attributed to the acclimation response of plants to high temperatures.

SAL095, SAL098, and SAL096 have demonstrated minimal changes in yield when subjected to HS. These genotypes also showed an increase in RL and LL, which may reflect an HS tolerance mechanism. A similar trend was reported by (Ezin et al., 2022). The possession of deep root systems is advantageous as it aids in water retention, hence reducing the rate of moisture loss and playing an essential role in preserving the freshness and extended shelf life of crops (Gumisiriza et al., 2023). Similar trends in yield were also observed in these genotypes for PW, LA, LW, and CC under HS. The reactions observed in these three genotypes led to enhanced performance under heat stress conditions, ultimately resulting in yield maintenance.

Conclusion

High temperatures in urban areas can cause a significant risk to lettuce production and food security for urban populations by adversely affecting the growth, yield, and marketability of lettuce. Therefore, it is essential to develop cultivars tolerant to high temperatures. The findings of our study indicate that various genotypes exhibited different reactions when exposed to high temperatures. Among the eight cultivars, SAL095 and SAL098 exhibited minimal changes in yield and growth parameters under HS conditions. This highlights the adaptability of both genotypes to high-temperature environments, which makes them advantageous for urban farming and the development of heat-stress tolerant cultivars.

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Conflict of Interest

The authors indicate no conflict of interest in this work.

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