



# Effects of Elevated Temperature on Agronomic, Morphological, Physiological and Biochemical Characteristics of Potato Genotypes: 1. Agronomic and Morphological traits

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## Abstract

Global elevated temperatures create uncertainties in crop yield production and sustainability, threatening potatoes' food security and sustainability roles. This has been among the primary research concerns necessitating the need to evaluate potato genotypes' response to elevated temperature under field conditions. This study assessed potato genotypes' agronomic and morphological responses to elevated temperatures. The experiments were conducted under field conditions in the 2022 and 2023 cropping seasons in a split-plot design. Two heat treatments were applied; a control treatment in which the plants received the field temperature of the experimental station, and a heat treatment in which the plants received a temperature of +6.0–10.0 °C depending on the date and time of day. The agronomic and morphological traits evaluated included tuber yield, mean tuber weight, days to emergence, plant height, number of stems per plant, days to physiological maturity, and tuber size distribution. The results showed significant ( $P < 0.01$ ) variations in the potato genotypes in response to elevated temperature in all traits except days to emergence. Elevated temperature promoted plant height by 36.94%, and days to physiological maturity by 2.55%, while reducing the number of stems per plant by 11.77% and days to emergence by 2.31%. Furthermore, elevated temperature increased total tuber yield by 25.38%, the number of tubers per plant by 18.75%, mean tuber weight by 8.89%, third-class tuber size distribution by 25.95% and malformed tuber ratio by 1.98%, while decreasing first-class tuber size distribution by 10.11%, second-class size distribution by 1.70% and marketable tuber yield by 4.22%. The results of this study demonstrated the impact of heat stress on potato tuber yield and size distribution. The study showed that temperatures around 27.0 °C to 33.0 °C effectively promoted total tuber yield, number of tubers per plant and mean tuber weight; thus, an increase in temperature within the effective range of potato plants promoted yield and yield-related components. This study demonstrates that open-sided field chambers can be a screening tool for heat tolerance of potato genotypes under field conditions. Potato genotypes with less variation in the traits between the heat and

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control treatment demonstrate heat tolerance and could be used as selection markers for heat-tolerant genotypes.

**Keywords** Elevated temperature · Heat stress · Morphological traits · Tuber size distribution

## Introduction

Potato (*Solanum tuberosum* L.) is one of the most widely produced agricultural products globally with an annual production of approximately 388 million tons in around 160 countries (FAO 2024). It is the food and vegetable crop that is considered one of the most promising crops for alleviating inadequate and unbalanced nutrition crisis because of its high yield potential and large production area (Aksoy et al. 2021; Zhou et al. 2023) making it the third most common food crop after corn and rice. The modern potato varieties are known to perform well under moderate temperatures around 20 °C with the optimum aerial biomass and underground tubers growth temperature within 20–25 °C and 15–20 °C respectively (Lee et al. 2020). However, the crop plant is very sensitive to environmental fluctuations, and even the same varieties show substantial variation in terms of morphological structure, yield, and quality characteristics under different ecological conditions (Van Dingenen et al. 2019; Hill et al. 2021; Van Nasir and Toth 2021).

In recent years, global climate dynamics have caused frequent and intense unfavourable weather conditions such as rising average annual temperatures. Heat stress is among the primary factors endangering the yield and productivity of cool-temperature crops including potatoes. The effects of heat stress have been significant on potatoes' morphology, physiological and biochemical processes, and transcriptional regulation, apart from the negative impact on yield (Momčilović 2019). Zhou et al. (2023) have shown that if the current trend of climate dynamics is not alleviated, potato yield is expected to decline by up to 30% due to heat stress. This threatens the food security role of crops, especially in areas where potatoes contribute about 45% of agriculture production (Naawe and Caliskan 2021; Devaux et al. 2021).

Heat stress phenomena result in morphological, physiological, and biochemical changes (Ávila-Valdés et al. 2020) with varying degrees of effect on potato yield. Potato plants' response to the impact of temperature depends on the cultivar and growth stage (Mokrani et al. 2023). Studies have reported the effect of the rise in temperature on the leaf area and biomass, tuber initiation, and tuber yield of potatoes (Lee et al. 2020). Demirel et al. (2020) stated that climate change will cause high-temperature stress in potatoes resulting in severe yield loss. In the temperate climate, a temperature rise is speculated to promote potato yield (Ávila-Valdés et al. 2020), while at the same time in the tropical and subtropical climates, a temperature rise negatively impacts potato crop yield (Hancock et al. 2014). Under control conditions, Kim and Lee (2019) found that low night temperatures facilitated tuber initiation and increased tuber sizes, while Lee et al. (2020) observed a positive effect of concurrent elevation of temperature and CO<sub>2</sub> concentration within the effective

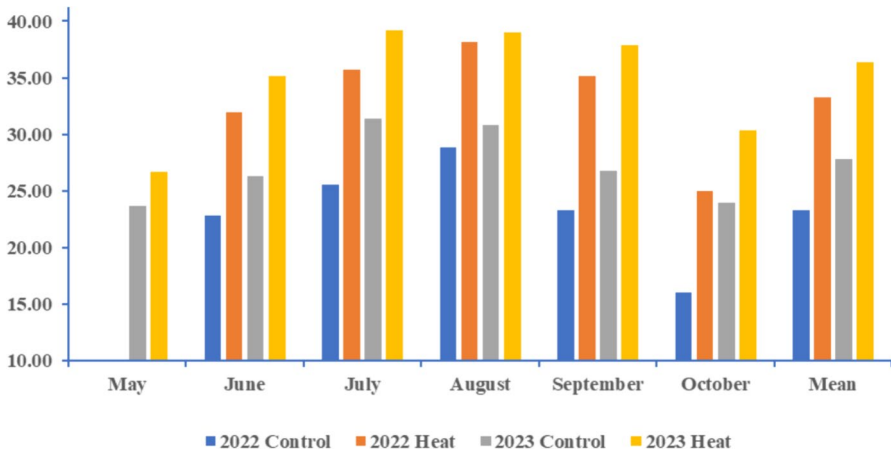
range on potato growth, net photosynthetic rate, leaf area, biomass, and tuber yield. Heat stress applied to the potato's belowground parts causes distinct tuber deformation, secondary growth, and loss of tuber skin colour without affecting the leaf photosynthetic system (Zhou et al. 2023). However, when heat stress is applied on both aerial and below-ground parts, potato yields and quality are negatively affected by causing a reduction in tuber number and mass, increased tuber disorders ratio, and compromised tuber processing and nutritional quality (Mokrani et al. 2023; Zhou et al. 2023). Heat tolerance potato cultivars have been characterised by higher (plant height, growth rate, chlorophyll b content, photosynthetic rate, stomatal conductance, transpiration rate, tuber number, and tuber yield) and lower levels of cell membrane injury (Zhang et al. 2024) while resulting in drastic yield and quality loss in susceptible varieties. However, very few field studies have been conducted on the impact of high temperatures on potatoes (Ávila-Valdés et al. 2020).

In recent times, many potato production zones have been characterised by unpredictability in their weather conditions (Divya et al. 2021, Ademe et al. 2024), especially regarding temperature rise. The sustainability of potato production is hence an essential target and the concern of potato breeders and farmers. Methods of breeding high-yielding, stable, and stress-tolerant potato genotypes to meet global food needs is a main foresight as a long-term adaptation strategy for sustainable food security. Little is however known about potato genotypes' response to heat stress under field conditions. Therefore, this study was conducted to determine the morphological and agronomic behaviour of potato breeding lines subjected to two different temperatures, which aimed to develop heat-tolerant climate-adapted potato varieties. This will enhance the understanding of the heat stress-mediated response of potato genotypes under field conditions.

## Materials and Methods

### Plant Materials, Experimental Area, and Conditions

A total of 29 putative potato genotypes (25 advanced potato lines and 4 standard cultivars) (Supplementary Table 1) were selected from the Potato Breeding Program of the Faculty of Agricultural Sciences and Technologies, Nigde Ömer Halisdemir University, Türkiye. These genotypes were subjected to a 2-year (2022 and 2023 potato growing seasons) field experiment at the experimental site of the Faculty of Agricultural Sciences and Technologies at Nigde Ömer Halisdemir University located at 37.9698° N and 34.6766° E and an elevation of 1244 m above sea level. The site is characterised by an annual average temperature of 10.3 °C and precipitation of 338 mm. The soil properties of the experimental area are detailed in Supplementary Table 2, while Fig. 1 presents the average temperatures during the study period. The experiment was conducted in a split-plot in a randomised complete block design (RCBD) with the production environment as the main plot (treatments), a 6-m distance between the treatments and the genotypes as sub-plots, each with four replications. Two heat treatments were applied; a control treatment in which the plants received the field temperature of the experimental station and a heat



**Fig. 1** Average monthly temperature (°C) during the field studies

stress treatment in which the plants received a temperature of +6.0–10.0 °C depending on the date and time of day. The heat stress treatment was applied by creating a plastic chamber measuring 22.5 m in length, 14.0 m in width, and which had a ridge height of 4.6 m. To ensure proper ventilation, ventilation flaps with 50 mesh nets were installed on all four sides. For the first 3 weeks after planting, the ventilation flaps were adjusted to create a temperature difference of approximately 6.0–10 °C higher than the natural environment in the control area, using the Nigde Ömer Halisdemir University Meteorological system as a baseline for the adjustment. This temperature gradient was maintained throughout the field study period. The experiment was manually planted at a density of 10 tubers per plot, with one row per plot and an inter-row and intra-row space of 70 cm × 30 cm. Each block replication comprised a length of 300 cm and 30 cm between replication blocks. The experiment was irrigated using drip irrigation at 4-day intervals, except when it rained, in which irrigation was only supplied to the heat stress treatment, as the plastic chambers prevented rainwater from reaching this plot. An ET-176 temperature and humidity data logger (with a precision of  $\pm 0.1$  °C and  $\pm 1\%$ ) kept 1 m above ground was used to record the temperature and relative humidity of the heat stress treatment, while the data for the control conditions were obtained from the Nigde Ömer Halisdemir University meteorological station. The experimental field was weeded regularly until 15 days before harvesting time.

### Environmental Conditions of the Experiments

The two growing seasons were characterised by different environmental conditions (Fig. 1). For the control conditions (normal temperature; CT), the first growing season S1 (2022) was characterised by a lower mean temperature, higher relative humidity (RH), and less rainfall (supplementary Table 3). The RH was highest in June and October, while the lowest RH occurred from late July to mid-August.

The second season S2 (2023) was characterised by high mean temperature (Fig. 1), higher rains (Supplementary Table 3) and peak RH from planting to mid-June and around the end of October. S1 had a more stable temperature than S2 throughout the season. The mean temperature of the heat stress (elevated temperature treatment; HT) was higher in the S2 than in the S1. The plastic materials used to create the temperature increase in stressful conditions prevented rains in the HT condition (Supplementary Table 3). In S1, the mean temperature for CT and HT was around 25.00 °C and 31.21 °C during the tuber initiation and bulking stages, while in S2, the mean temperature for CT and HT during tuber initiation and bulking was around 28.22 °C and 34.78 °C respectively.

## Data Measurement

### Day to Emergence (Days)

The time to emergence (days) was monitored after planting, and the emergence time of the potato genotypes was determined when 75% of the plants emerged for the control and heat treatment.

### Days to Physiological Maturity (Days)

The physiological maturation time was calculated from emergence to the date at which 75% of the plant leaves in each plot turned yellow.

### Number of Stems per Plant and Plant Height (cm)

During the flowering stage, the stems of five random plants per plot were counted and averaged as the number of stems per plant (NSP), while the height (PH) of five random plants per plot was measured using a tape measure at  $\pm 1$  cm accuracy.

## Agronomic Traits

The agronomic traits measured in this study included the tuber size grading (%), malformed tuber ratio, number of tubers per plant, mean tuber weight (g), marketable tuber yield (t/ha), and total tuber yield (t/ha). The potato tubers were graded in three; first-class tubers (> 50 mm), second-class tubers (30–50 mm), and third-class tubers (< 30 mm). The ratio of potato tubers with secondary growth or disordered forms was classified as malformed tubers ratio out of the total number of tubers per genotype. The number of tubers per plant was calculated by dividing the total number of tubers per plot by the number of plants per plot. Mean tuber weight (g) was calculated by dividing the weight of tubers per plot by the total number of tubers per plot. Marketable tuber yield (t/ha) was calculated by adding and converting the yield of first-class and second-class tubers in kilograms to tons per hectare. The total tuber yield (t/ha) was calculated by adding and converting the yield of first-class tubers,

second-class tubers, third-class tubers, and malformed tubers in kilograms to tons per hectare.

## Data Processing and Analysis

Excel 365 version was used to process all the data. The statistical analysis included analysis of variance (ANOVA) using Jamovi statistical software (version 2.3) and Origin Lab software (student version 2024). The ANOVA results were considered significant at  $P < 0.05$ , and Duncan's multiple-range test was used to perform mean comparisons.

## Results

### Effect of Elevated Temperature on the Phenological and Morphological Traits

A significant ( $P < 0.01$ ) variation in the days to emergence among the potato genotypes was observed for both control (CN) and heat (HT) in both seasons (Table 1). A significant ( $P < 0.05$ ) variation was observed between the years and year  $\times$  treatment interactions of the days to emergence (DE); however, no significant variation was observed between the CN and HT groups (Table 1). The elevated temperature caused a 2.04% increase in DE of HT over CN in S1 while a 0.79% decrease in DE of the HT over CN was observed in S2 (Table 2). This could suggest that temperature promoted growth by shortening the DE in S2. In both seasons, a significant ( $P < 0.01$ ) (Table 1) effect was observed among the genotypes, and between the CN and HT for physiological maturity (PM), number of stems per plant (NSP), and plant height (PH). The PM was observed to have significantly varied between the CN and HT with a 10.91% increase in the mean PM for the HT over the CN in S1, while in S2, an 8.36% decline in the mean PM was observed in HT over the CN (Table 2). The significant ( $P < 0.01$ ) variations observed in the PH in both seasons resulted in a 36.62% and 37.25% increase of the HT over CN in S1 and S2 respectively (Table 2). A 1.43% increase in NSP was observed in HT over the CN in S1; however, in S2, a 13.20% decline in the NSP was observed in HT over the CN (Table 2).

### Impact of Temperature on Tuber Yield and Yield Components

A significant variation in tuber number per plant (NTP) was observed among the genotypes in both the control (CN) group and the heat stress (HT) group in both seasons (Table 3). The NTP was consistently and significantly ( $P < 0.01$ ) higher in the HT group in all the genotypes than CN in S1 while in the S2 nine (9) out of 29 genotypes recorded higher NTP in the CN than the HT (Table 3). In S1, the NTP ranged from 3.96 tubers to 7.05 tubers with an average of 5.0 tubers for the CN, while for HT, NTP ranged from 5.1 tubers to 9.1 tubers with an average of 6.6 tubers, resulting in a 32% increase in NTP of the HT over the CN. In the second season (S2), the NTP ranged from 5.2 tubers to 9.5 tubers for the CN with an average of 7.3, whereas

**Table 1** Three-way mean square analysis of variance of the genotypes, treatment, year, and their interaction for the assessed traits of potato genotypes under elevated temperature and control treatment conditions

	Year	TRT	GEN	Year×TRT	Year×GEN	TRT×GEN	Year×TRT×GEN	Error	Total
DF	1	1	28	1	28	28	28	348	463
DE	53.12***	2.35 ns	10.93***	12.78*	3.45 ns	1.41 ns	2.06 ns	2.79	
PM	19552.03***	7.76**	10.64 ns	12,105.39***	13.99*	1.06	0.91 ns	8.84	
NSP	276.37***	20.83***	15.52***	27.86***	4.25**	2.15 ns	3.01 ns	2.22	
PH	6270.78***	60,262.69***	258.79***	196.69 ns	99.90 ns	78.44 ns	57.93 ns	75.58	
TTY	22,162.36***	3489.57***	1704.43***	12,205.97***	790.74***	321.45 ns	217.80 ns	314.02	
FCTD	85,909.56***	4902.58***	899.84***	2421.91***	338.11**	243.11 ns	312.53**	177.83	
SCTD	9723.76***	103.97*	466.32***	1243.70**	500.75***	288.65**	269.92**	108.58	
TCTD	72,364.01***	626.09***	160.61***	296.15**	113.66***	83.96**	109.06***	49.70	
DT	7117.69***	6640.85***	59.05*	3300.98***	59.41*	54.95 ns	61.73*	40.97	
NTP	181.34***	45.86***	17.72***	108.46***	8.54***	3.59 ns	2.25 ns	3.27	
MTW	5528.30***	3783.37***	421.21***	3.94 ns	447.99***	256.00**	197.60 ns	143.76	
TTY	7067.76***	1112.29**	603.76***	1283.57**	158.61**	180.69**	104.26 ns	92.80	
MTY	5731.35***	525.35**	498.55***	2307.98***	118.10 ns	140.54**	76.36 ns	81.16	

DE, days to emergence; PM, days to physiological maturity; PH, plant height; NSP, number of stems per plant; FCTD, first-grade tuber distribution; SCTD, second-class tuber distribution; TCTD, third-class tuber distribution; DT, malformed tuber ratio; TTY, total tuber yield; MTY, marketable tuber yield; MTW, mean tuber weight; GEN, genotype; TRT, treatment; DF, degree of freedom; \* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ , ns, not significant ( $P \geq 0.05$ )

**Table 2** Mean comparison of the day-to-emergence (DE), physiological maturity (PM), number of stems per plant (NSP) and plant height (PH) between control (CN) and heat (HT) treatments of the potato genotypes for 2022 and 2023 cropping seasons

Traits	Year	Treatment	Mean $\pm$ std	Effect of elevated temperature
Days to emergence (days)	1	Heat	25.00 $\pm$ 1.43	2.04% increase
		Control	24.50 $\pm$ 1.36	
	2	Heat	23.99 $\pm$ 2.56	0.79% decrease
		Control	24.18 $\pm$ 1.52	
Physiological maturity (days)	1	Heat	106.47 $\pm$ 1.36	10.91% increase
		Control	96.00 $\pm$ 1.43	
	2	Heat	109.24 $\pm$ 3.81	8.36% decrease
		Control	119.20 $\pm$ 3.84	
Number of stems per plant	1	Heat	4.98 $\pm$ 1.67	1.43% increase
		Control	4.91 $\pm$ 1.50	
	2	Heat	6.05 $\pm$ 1.67	13.20% decrease
		Control	6.97 $\pm$ 2.23	
Plant height (cm)	1	Heat	80.17 $\pm$ 9.92	36.62% increase
		Control	58.68 $\pm$ 7.43	
	2	Heat	88.83 $\pm$ 11.07	37.25% increase
		Control	64.72 $\pm$ 8.56	

Four replicates were averaged and statistically analysed. Values are the mean  $\pm$  standard deviation

in the HT, the NTP ranged from 5.3 to 10.8 for the HT with an average of 6.9, resulting a 5.5% increase in the NTP of the CN over the HT (Table 3).

The mean tuber weight (MTW) varied significantly ( $P < 0.01$ ) (Table 1) among the genotypes in both the CN and HT groups with the HT group recording higher average MTW than the CN group in both seasons (Table 4). In S1, the MTW of the CN ranged from 60.33 g to 75.28 g with an average of 68.12 g, while the HT group ranged from 57.96 g to 83.39 g with an average of 73.65 g, resulting in an 8.12% increase in the MTW of HT over the CN group. In S2, MTW varied from 40.60 g to 82.39 g with an average of 61.03 g in the CN, while in the HT group, it ranged from 49.09 g to 95.20 g with an average of 66.93 g, and an average increase of 9.67% in the MTW of the tubers in the HT group over the CN. In the S1, all but one genotype had higher MTW in the HT than in the CN, while in the S2, 13 genotypes recorded higher mean tuber weight in the CN than in the heat treatment (Table 4). The results from the ANOVA (Table 1) revealed that these differences in MTW were due to genotype, treatment, and the interaction between genotypes and treatment (Table 1). Thus, heat stress treatment caused an increase of 8.90% on average in the mean tuber weight of potato genotypes in both seasons.

A significant ( $P < 0.01$ ) variation in the total tuber yield (TTY) was observed among the tested potato genotypes in both seasons for the CN and HT (Table 1, Table 5). The TTY was significantly ( $P < 0.01$ ) higher in the HT than in the CN in S1, while there was no significant difference between the HT and CN in S2. In



**Table 3** Number of tubers per plant (NTP) of the control (CN) and heat (HT) treatments in the 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.20	4.9±1.22 abc	6.4±1.27 bcd	6.3±1.32 abc	6.6±2.28 abc
MEÇ1302.15	3.4±1.21 c	5.4±1.10 abcd	6.4±1.45 c	2.9±1.27 c
MEÇ1302.18	4.6±0.89 abc	5.2±0.65 abcd	7.2±1.94 c	6.7±1.32 abc
MEÇ1302.20	3.9±0.80 bc	5.1±0.98 bcd	5.6±0.94 c	5.3±1.22 abc
MEÇ1305.05	6.1±1.46 abc	7.4±0.91 cd	5.5±1.42 abc	5.5±1.16 abc
MEÇ1406.07	6.6±1.15 ab	8.1±1.02 ab	9.5±2.10 abc	9.3±2.23 ab
MEÇ1407.05	7.1±1.04 a	8.7±2.70 abcd	9.1±2.02 ab	10.8±3.49 a
MEÇ1407.08	3.9±0.53 bc	5.0±0.43 abcd	6.8±1.48 c	5.2±0.61 abc
MEÇ1407.17	6.6±0.47 ab	6.8±0.84 bcd	5.9±1.83 abc	4.1±1.89 bc
MEÇ1409.09	4.5±1.55 abc	7.3±1.59 abcd	6.8±0.72 abc	8.7±0.79 abc
MEÇ1411.06	4.4±1.63 abc	5.5±0.45 a	10.2±2.92 bc	9.6±1.64 ab
MEÇ1501.02	5.2±0.56 abc	5.6±0.96 abcd	8.2±0.36 bc	5.6±2.30 abc
MEÇ1502.04	6.0±1.17 abc	7.7±0.41 abcd	6.3±1.06 abc	7.8±2.19 abc
MEÇ1502.15	4.7±1.38 abc	6.1±0.99 abcd	7.5±1.14 abc	9.1 2.98 abc
MEÇ1502.16	4.9±1.33 abc	6.9±0.98 abcd	7.6±1.13 abc	7.7±0.47 abc
MEÇ1502.21	5.0±0.97 abc	6.7±1.79 abcd	7.1±1.79 abc	7.9±1.96 abc
MEÇ1502.25	4.6±1.00 abc	5.8±1.61 abc	9.3±1.26 abc	7.9±3.81 abc
MEÇ1504.01	6.1±1.56 abc	7.9±2.40 abc	9.3±3.15 abc	8.7±1.66 abc
MEÇ1505.02	5.1±1.40 abc	7.0±0.74 abcd	6.3±1.88 abc	5.7±1.92 abc
MEÇ1505.06	5.1±1.62 abc	9.0±1.83 abcd	7.0±0.99 a	7.9±2.39 abc
MEÇ1505.07	6.8±1.32 ab	7.7±1.33 abcd	8±1.33 abc	6.1±1.70 abc
MEÇ1525.02	4.2±0.56 abc	5.1±0.59 d	5.2±1.79 c	5.9±1.45 abc
MEÇ1525.03	4.3±1.15 abc	6.1±1.33 abcd	6.9±1.35 abc	6.8±1.19 abc
MEÇ1525.17	4.3±0.81 abc	6.7±1.29 bcd	5.7±0.77 abc	2.9±1.12 c
MEÇ1530.02	4.5±0.82 abc	6.3±1.01 abc	9.2±1.05 abc	6.4±0.76 abc
Agria	4.8±0.33 abc	8.0±1.25 abcd	8.8±2.11 abc	10.1±4.42 ab
Desiree	4.2±1.11 abc	5.8±1.49 abcd	6.5±1.31 abc	6.9±0.46 abc
Petek	5.2±1.62 abc	6.2±1.13 cd	5.4±1.10 abc	7.1±0.20 abc
Russet Burbank	5.3±1.08 abc	7.4±2.22 abcd	6.7±0.95 abc	5.7±2.54 abc
Average	5.0	6.6	7.3	6.9

Values for the number of tubers per plant are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

S1, the TTY ranged from 9.41 to 57.02 t/h for the CN with an average yield of 24.86 t/h, while the HT ranged from 11.79 to 62.46 t/h with an average of 31.45 t/h (Table 5), resulting in a 26.51% increase in TTY in HT over the CN treatment. All the genotypes except MEÇ1302.15 and MEÇ1407.08 recorded higher TTY in HT than in CN in S1 (Table 5). In the S2, the TTY for the CN ranged from 9.17 to 26.42 t/h with an average of 20.38 t/h, while the TTY of the HT ranged from

**Table 4** Mean tuber weight (g) in the control (CN) and heat (HT) treatments in the 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.20	69.83 ± 3.64 ab	71.20 ± 7.36 ab	67.81 ± 7.18 abcd	95.19 ± 36.49 a
MEÇ1302.15	65.59 ± 5.62 ab	75.19 ± 4.41 ab	58.40 ± 5.46 abcd	95.46 ± 26.54 a
MEÇ1302.18	72.19 ± 0.73 ab	73.66 ± 5.89 ab	42.33 ± 8.43 bcd	59.31 ± 8.33 ab
MEÇ1302.20	62.83 ± 9.47 ab	57.96 ± 20.67 b	66.95 ± 15.71 abcd	68.78 ± 10.88 ab
MEÇ1305.05	60.33 ± 7.48 ab	63.38 ± 7.38 ab	45.57 ± 6.52 bcd	66.15 ± 13.98 ab
MEÇ1406.07	69.85 ± 9.48 ab	76.54 ± 3.63 ab	36.13 ± 5.12 d	54.85 ± 10.33 ab
MEÇ1407.05	68.99 ± 2.81 ab	69.38 ± 2.82 ab	79.30 ± 3.48 a	79.07 ± 22.70 ab
MEÇ1407.08	65.82 ± 8.93 ab	74.23 ± 3.77 ab	61.00 ± 11.58 abcd	64.53 ± 3.41 ab
MEÇ1407.17	68.82 ± 3.72 ab	77.09 ± 7.64 ab	63.48 ± 21.17 abcd	57.15 ± 11.82 ab
MEÇ1409.09	70.91 ± 4.97 ab	80.49 ± 6.62 ab	74.64 ± 19.83 ab	64.84 ± 11.14 ab
MEÇ1411.06	67.76 ± 3.61 ab	72.82 ± 3.90 ab	51.92 ± 13.23 abcd	70.84 ± 5.33 ab
MEÇ1501.02	70.22 ± 2.10 ab	81.93 ± 8.69 a	62.21 ± 14.08 abcd	58.55 ± 10.15 ab
MEÇ1502.04	61.42 ± 6.98 ab	75.74 ± 3.79 ab	67.56 ± 11.34 abcd	75.85 ± 11.17 ab
MEÇ1502.15	69.17 ± 5.80 ab	73.44 ± 2.78 ab	82.39 ± 14.17 a	82.23 ± 12.15 ab
MEÇ1502.16	74.05 ± 0.55 ab	71.79 ± 8.01 ab	57.46 ± 11.13 abcd	61.36 ± 12.31 ab
MEÇ1502.21	67.55 ± 7.94 ab	70.52 ± 9.33 ab	70.20 ± 10.13 abc	62.73 ± 2.25 ab
MEÇ1502.25	74.46 ± 4.22 ab	71.24 ± 4.69 ab	64.46 ± 17.91 abcd	56.06 ± 6.02 ab
MEÇ1504.01	75.28 ± 2.58 a	72.74 ± 1.38 ab	79.78 ± 3.99 a	59.28 ± 11.58 ab
MEÇ1505.02	69.41 ± 4.97 ab	72.79 ± 1.18 ab	49.53 ± 6.20 abcd	58.49 ± 4.35 ab
MEÇ1505.06	65.94 ± 3.22 ab	69.14 ± 4.77 ab	51.93 ± 9.55 abcd	49.08 ± 3.48 b
MEÇ1505.07	68.32 ± 2.62 ab	71.96 ± 2.68 ab	64.46 ± 11.67 abcd	59.84 ± 9.87 ab
MEÇ1525.02	67.69 ± 3.28 ab	75.12 ± 9.36 ab	50.26 ± 6.95 abcd	65.74 ± 12.73 ab
MEÇ1525.03	53.92 ± 22.92 b	69.14 ± 2.71 ab	65.68 ± 5.71 abcd	57.39 ± 7.37 ab
MEÇ1525.17	70.37 ± 1.71 ab	75.43 ± 5.99 ab	82.33 ± 15.48 a	79.49 ± 7.49 ab
MEÇ1530.02	65.44 ± 3.02 ab	79.26 ± 5.59 ab	69.88 ± 9.02 abc	63.88 ± 14.73 ab
Agria	67.77 ± 12.40 ab	83.39 ± 13.15 a	40.60 ± 9.47 cd	65.67 ± 11.71 ab
Desiree	68.40 ± 9.23 ab	78.31 ± 5.29 ab	45.28 ± 9.51 bcd	74.13 ± 11.03 ab
Petek	69.48 ± 3.03 ab	73.25 ± 9.69 ab	62.28 ± 14.92 abcd	63.55 ± 12.33 ab
Russet Burbank	73.66 ± 6.04 ab	78.61 ± 6.89 ab	55.98 ± 15.9 abcd	71.42 ± 19.05 ab
Average	68.12	73.65	61.03	66.93

Values for the mean tuber weight are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

8.81 to 29.52 t/h with an average of 20.15 t/h (Table 5); no significant ( $P > 0.05$ ) and consistent variation was observed between the treatments (Table 1). However, an average of 1.13% increase in TTY in CN over the HT was observed. Furthermore, the TTY was higher in S1 than in S2 for both HT and CN treatments, with a 4.48 t/h decline in TTY for CN and an 11.30 t/h decline in HT (Table 5).

**Table 5** Total tuber yield (t/ha) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.2	23.62 ± 3.90 abcde	33.80 ± 5.77 bcdef	26.42 ± 2.72 ab	22.49 ± 3.20 abcd
MEÇ1302.15	22.48 ± 5.92 abcde	22.01 ± 4.00 cdef	16.07 ± 4.57 abcd	10.71 ± 4.08 cd
MEÇ1302.18	18.26 ± 2.46 abcde	34.50 ± 6.90 bcdef	17.97 ± 7.01 abcd	24.04 ± 4.09 abc
MEÇ1302.2	25.70 ± 8.26 abcde	27.73 ± 3.51 bcdef	24.88 ± 5.50 abc	19.28 ± 4.29 abcd
MEÇ1305.05	19.25 ± 5.64 abcde	26.52 ± 4.17 bcdef	12.14 ± 2.25 bcd	16.30 ± 3.69 abcd
MEÇ1406.07	12.83 ± 4.89 cde	13.26 ± 5.01 ef	11.66 ± 1.41 cd	16.78 ± 1.88 abcd
MEÇ1407.05	24.44 ± 2.18 abcde	36.20 ± 8.26 bcde	23.92 ± 7.57 abc	19.52 ± 8.01 abcd
MEÇ1407.08	36.34 ± 2.00 a	31.70 ± 9.22 bcdef	24.64 ± 6.06 abc	22.97 ± 1.97 abcd
MEÇ1407.17	48.26 ± 4.21 ab	57.02 ± 5.06 ab	27.97 ± 5.65 a	23.45 ± 4.80 abc
MEÇ1409.09	21.78 ± 2.36 abcde	27.65 ± 6.88 bcdef	23.21 ± 11.80 abcd	15.83 ± 3.47 abcd
MEÇ1411.06	31.08 ± 4.92 abc	44.64 ± 4.38 abc	22.26 ± 3.82 abcd	21.42 ± 2.49 abcd
MEÇ1501.02	20.65 ± 4.44 abcde	37.01 ± 9.92 bcd	20.59 ± 3.50 abcd	21.19 ± 4.61 abcd
MEÇ1502.04	26.07 ± 4.34 abcde	22.15 ± 4.19 cdef	19.16 ± 8.93 abcd	13.45 ± 8.27 bcd
MEÇ1502.15	19.10 ± 2.15 abcde	26.21 ± 5.44 bcdef	23.09 ± 5.37 abcd	24.76 ± 6.24 abc
MEÇ1502.16	29.19 ± 4.76 abcd	62.46 ± 8.70 a	23.92 ± 6.18 abc	29.52 ± 2.86 a
MEÇ1502.21	21.73 ± 1.36 abcde	36.16 ± 6.39 bcde	22.14 ± 6.35 abcd	25.83 ± 3.69 ab
MEÇ1502.25	15.64 ± 6.07 bcde	35.80 ± 3.81 bcde	20.35 ± 11.14 abcd	21.19 ± 0.85 abcd
MEÇ1504.01	24.95 ± 9.85 abcde	22.90 ± 8.47 cdef	20.59 ± 4.19 abcd	18.92 ± 3.42 abcd
MEÇ1505.02	16.39 ± 5.50 bcde	29.15 ± 1.56 bcdef	14.99 ± 9.56 abcd	21.42 ± 4.02 abcd
MEÇ1505.06	27.64 ± 4.67 abcde	30.46 ± 4.28 bcdef	22.61 ± 2.96 abcd	20.47 ± 2.17 abcd
MEÇ1505.07	26.04 ± 2.04 abcde	29.57 ± 6.83 bcdef	23.69 ± 7.59 abc	19.04 ± 7.03 abcd
MEÇ1525.02	27.49 ± 10.9 abcde	46.69 ± 6.88 ab	22.61 ± 2.97 abcd	23.45 ± 5.89 abc
MEÇ1525.03	49.63 ± 3.33 abcde	23.31 ± 18.49 bcdef	21.07 ± 5.52 abcd	17.85 ± 2.66 abcd
MEÇ1525.17	25.49 ± 2.27 abcde	42.61 ± 9.70 abc	26.07 ± 9.81 ab	25.95 ± 1.37 ab
MEÇ1530.02	29.17 ± 2.79 abcd	32.74 ± 3.76 bcdef	24.16 ± 8.23 abc	23.57 ± 4.61 abc
Agria	9.41 ± 5.85 e	11.79 ± 2.98 f	9.17 ± 5.01 d	18.69 ± 3.84 abcd
Desiree	25.13 ± 4.44 abcde	25.46 ± 1.39 bcdef	12.38 ± 5.01 bcd	19.16 ± 4.79 abcd
Petek	22.27 ± 7.96 abcde	32.96 ± 8.67 bcdef	18.21 ± 1.55 abcd	18.09 ± 11.74 abcd
Russet Burbank	11.95 ± 2.13 de	13.83 ± 2.40 def	14.88 ± 3.03 abcd	8.81 ± 1.59 d
Average	24.86	31.45	20.38	20.15

Values for the tuber yield are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

Similar to the TTY, the marketable tuber yield (MTY) was significantly ( $P < 0.05$ ) different between the HT and CN treatment groups in both seasons. In S1, the MTY of the CN ranged from 7.62 to 46.67 t/h with an average of 22.24 t/h while the HT ranged from 8.33 to 50.65 t/h with an average of 25.28 t/h (Table 6). In the S2, the MTY ranged from 9.17 to 27.98 t/h with an average of 17.38 t/h while the HT group ranged from 5.24 to 22.14 t/h with an average of 14.27 t/h.

**Table 6** Marketable tuber yield (t/ha) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.20	22.72 ± 7.36 ab	29.42 ± 3.63 abcd	26.43 ± 36.49 ab	16.42 ± 7.18 abcd
MEÇ1302.15	20.85 ± 4.45 ab	16.83 ± 5.62 bcd	16.07 ± 26.54 abcd	5.24 ± 5.46 cd
MEÇ1302.18	17.11 ± 5.89 b	27.44 ± 0.73 abcd	17.98 ± 8.32 abcd	17.85 ± 8.43 abc
MEÇ1302.20	24.46 ± 20.69 ab	24.13 ± 9.46 bcd	24.88 ± 10.89 abc	12.98 ± 15.71 abcd
MEÇ1305.05	17.33 ± 7.38 b	21.95 ± 7.47 bcd	12.14 ± 13.98 bcd	10.48 ± 6.52 abcd
MEÇ1406.07	10.66 ± 3.63 b	9.86 ± 9.48 cd	11.67 ± 10.34 cd	10.11 ± 5.12 abcd
MEÇ1407.05	23.93 ± 2.82 ab	33.55 ± 2.81 abc	23.93 ± 22.77 abc	13.69 ± 3.48 abcd
MEÇ1407.08	34.81 ± 9.78 ab	28.12 ± 2.52 abcd	24.64 ± 3.46 abc	16.42 ± 11.58 abcd
MEÇ1407.17	50.26 ± 7.63 ab	36.80 ± 3.71 ab	27.98 ± 11.82 a	16.19 ± 21.17 abcd
MEÇ1409.09	20.16 ± 6.62 ab	21.02 ± 4.96 bcd	23.21 ± 11.13 abcd	9.29 ± 19.83 abcd
MEÇ1411.06	29.96 ± 3.92 ab	39.37 ± 3.68 ab	22.26 ± 5.33 abcd	15.35 ± 13.23 abcd
MEÇ1501.02	19.86 ± 8.69 ab	25.44 ± 2.14 bcd	20.59 ± 10.16 abcd	14.04 ± 14.08 abcd
MEÇ1502.04	24.11 ± 3.78 ab	16.91 ± 6.98 bcd	19.17 ± 11.17 abcd	7.86 ± 11.33 bcd
MEÇ1502.15	17.67 ± 2.78 ab	22.63 ± 5.84 bcd	22.09 ± 12.15 abcd	18.92 ± 14.17 ab
MEÇ1502.16	26.09 ± 8.01 ab	50.65 ± 0.54 a	23.93 ± 12.31 abc	22.14 ± 11.13 a
MEÇ1502.21	20.20 ± 9.33 ab	28.75 ± 7.93 abcd	22.14 ± 2.24 abcd	19.64 ± 10.13 ab
MEÇ1502.25	12.98 ± 4.69 b	28.87 ± 4.22 abcd	20.36 ± 6.01 abcd	15.11 ± 17.91 abcd
MEÇ1504.01	20.96 ± 1.38 ab	21.28 ± 2.57 bcd	20.59 ± 11.59 abcd	12.26 ± 3.99 abcd
MEÇ1505.02	15.30 ± 1.17 b	24.44 ± 4.96 bcd	14.99 ± 4.35 abcd	14.64 ± 6.25 abcd
MEÇ1505.06	26.33 ± 4.76 ab	26.36 ± 3.22 bcd	22.62 ± 3.47 abcd	13.80 ± 9.55 abcd
MEÇ1505.07	23.49 ± 2.68 ab	26.63 ± 2.62 bcd	22.69 ± 9.87 abc	12.73 ± 1.67 abcd
MEÇ1525.02	26.60 ± 9.36 ab	35.82 ± 3.28 ab	22.62 ± 12.73 abcd	16.30 ± 6.95 abcd
MEÇ1525.03	46.67 ± 2.71 a	19.53 ± 22.92 bcd	21.07 ± 7.36 abcd	15.78 ± 5.71 abcd
MEÇ1525.17	23.60 ± 5.99 ab	29.86 ± 1.71 abcd	25.07 ± 7.49 ab	19.64 ± 15.48 ab
MEÇ1530.02	28.12 ± 5.59 ab	25.36 ± 3.02 bcd	23.17 ± 14.73 abc	16.07 ± 9.02 abcd
Agria	7.62 ± 13.15 b	8.33 ± 12.47 d	9.17 ± 11.72 d	12.38 ± 9.467 abcd
Desiree	23.38 ± 5.28 ab	20.16 ± 9.23 bcd	12.38 ± 11.32 bcd	13.33 ± 9.51 abcd
Petek	20.01 ± 9.69 ab	23.82 ± 3.03 bcd	18.21 ± 12.33 abcd	12.14 ± 14.92 abcd
Russet Burbank	10.23 ± 6.88 b	9.77 ± 6.03 cd	14.88 ± 19.51 abcd	12.97 ± 15.94 d
Average	22.24	25.28	17.38	14.27

The marketable tuber yield values are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

Contrary to S1 where the MTY of the HT group was higher in almost all the genotypes than the MTY of the CN group, in S2, the MTY was higher in CN than in the HT in almost all the genotypes (Table 6). This trend was due to the tuber sizes in S2 where tuber sizes were generally small compared to S1, although the number of tubers was significantly higher in the HT in S2; most of the tubers

were unmarketable. This resulted in a 3.03 t/h increase in the MTY of HT over CN in S1 but a 3.12 t/h decline in the MTY of the HT compared to the CN in S2.

### Effect of Elevated Temperature on the Tuber Size Distribution and Malformed Tuber Ratio

A significant ( $P < 0.01$ ) variation was observed for the tuber size distribution and the malformed tuber ratio among the genotypes for both the CN and HT stress treatment groups in both seasons (Table 1). The tuber distribution and malformed tuber ratio also significantly ( $P < 0.05$ ) varied for the year \* treatment, and year \* genotype interaction (Table 1). A high percentage of first-class tuber size distribution was observed in the CN over the HT in both seasons (Table 7). In S1, the percentage first-class size distribution ranged from 26.7 to 89.16% with an average of 71.95% for the CN group while the HT ranged from 32.75 to 80.19% with an average of 60.87% (Table 7). In the S2, the percentage first-class size distribution ranged from 23.77 to 54.50% with an average of 40.16% for the CN group while for the HT group, the percentage first-class size distribution ranged from 24.6 to 50.38% with an average of 38.23% (Table 7). In S1, 23 genotypes recorded higher first-class tubers in the CN over the HT, while in S2, 21 genotypes recorded higher first-class tubers in the CN than in the HT. Thus, elevated temperature caused a 15.40% and 4.81% reduction in the first-class tuber size distribution in the first and second seasons respectively.

As revealed in Table 8, in S1, the second-class tuber size ranged from 7.58 to 69.19% with an average of 22.27% for the CN while in the HT it ranged from 4.84 to 54.82% with an average of 24.60%. In S2 on the other hand, the second-class tuber size ranged from 25.33 to 58.45% for the CN and 16.05 to 42.62% for the HT with an average of 34.70% and 30.48% for the CN and HT respectively (Table 8). Thus, the second-class tuber size distribution increased by 10.46% under the HT condition in S1 while in S2, it decreased by 12.16% under the HT conditions. This variation in the second-class tuber size distribution was significant ( $P < 0.01$ ) among the genotypes for both CN and HT and between the CN and HT in both seasons (Table 8).

The third-class tuber distribution ranged from 0.34 to 4.28% with an average of 1.72%, and 0.44 to 8.03% with an average of 2.35% for the CN and HT respectively in S1 (Table 9). The percentage of the third-class tuber distribution was higher in S2 than in S1. In S2, third-class tuber ranged from 13.45 to 41.14% with an average of 25.23% for the CN and 13.48 to 54.21% with an average of 29.08% for the HT (Table 9). Thus, the elevated temperature significantly ( $P < 0.01$ ) (Table 1) increased the third-class tuber distribution by 36.63% and 15.26% in the first and second seasons respectively (Table 9). Heat stress increased tuber secondary growth on the tubers resulting in a significantly ( $P < 0.01$ ) higher malformed tubers in the HT than the CN in both seasons (Table 1, Table 10). The malformed tuber ratio ranged from 0.0 to 9.47% with an average of 2.68% and 0.89 to 30.49% with an average of 15.87% for the CN and HT, respectively, in S1. In S2, the malformed tuber ratio ranged from 0.0 to 23.693% with an average of 1.28% for the CN and from 0.31 to 42.75% with an average of 2.21% for the HT (Table 10).

**Table 7** First-class tuber distribution (%) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.20	71.49 ± 8.11 bcdef	73.96 ± 14.11 ab	51.05 ± 6.75 ab	50.38 ± 7.18 ab
MEÇ1302.15	77.22 ± 3.36 abc	47.92 ± 15.45 cdefg	43.92 ± 6.82 abcde	50.14 ± 12.3 abc
MEÇ1302.18	76.74 ± 6.66 abc	56.65 ± 6.54 abcdefg	29.63 ± 11.29 fg	34.76 ± 8.35 defghij
MEÇ1302.2	75.67 ± 6.95 abcd	72.29 ± 6.51 abc	49.48 ± 11.64 ab	40.50 ± 5.95 abcdefghi
MEÇ1305.05	60.38 ± 8.04 def	69.30 ± 9.75 abc	31.70 ± 7.17 efg	44.96 ± 10.44 abcdefg
MEÇ1406.07	26.70 ± 26.89 g	39.70 ± 15.39 efg	28.00 ± 6.91 fg	24.60 ± 4.39 j
MEÇ1407.05	83.13 ± 7.68 ab	73.61 ± 12.76 ab	47.13 ± 9.34 abcd	46.08 ± 21.68 abcdef
MEÇ1407.08	80.81 ± 8.87 ab	73.03 ± 13.37 ab	39.15 ± 14.49 bcdef	40.53 ± 6.77 abcdefghi
MEÇ1407.17	82.49 ± 10.46 ab	60.32 ± 9.22 abcdef	46.69 ± 7.10 abcd	32.31 ± 7.84 fghij
MEÇ1409.09	83.83 ± 12.93 ab	63.65 ± 15.85 abcde	46.85 ± 8.15 abcd	37.32 ± 13.66 bcdefghij
MEÇ1411.06	81.19 ± 2.85 ab	67.84 ± 23.44 abcd	34.56 ± 10.47 cdefg	43.64 ± 5.01 abcdefgh
MEÇ1501.02	76.92 ± 7.55 abc	53.24 ± 13.32 bcdefg	34.53 ± 5.35 cdefg	30.65 ± 7.58 ghij
MEÇ1502.04	81.25 ± 10.61 ab	43.61 ± 21.99 defg	46.25 ± 11.58 abcd	40.35 ± 4.97 abcdefghi
MEÇ1502.15	80.72 ± 6.46 ab	73.08 ± 13.13 ab	54.50 ± 5.66 a	52.57 ± 9.61 a
MEÇ1502.16	68.78 ± 4.74 bcdef	52.50 ± 4.81 bcdefg	40.77 ± 10.54 abcdef	34.35 ± 8.64 efg hij
MEÇ1502.21	62.05 ± 7.35 cdef	53.77 ± 11.25 bcdefg	49.71 ± 10.07 ab	48.82 ± 4.15 abcd
MEÇ1502.25	56.45 ± 18.86 f	62.95 ± 12.72 abcde	44.25 ± 18.81 abcde	38.51 ± 9.69 abcdefghij
MEÇ1504.01	63.33 ± 7.42 cdef	80.10 ± 4.44 a	52.00 ± 5.17 ab	28.76 ± 7.69 ij
MEÇ1505.02	73.31 ± 6.36 bcde	68.92 ± 17.98 abc	23.77 ± 6.3 g	38.44 ± 3.74 abcdefghij
MEÇ1505.06	71.34 ± 8.95 bcdef	63.49 ± 8.56 abcde	34.21 ± 17.14 defg	28.28 ± 2.69 ij
MEÇ1505.07	64.23 ± 12.29 cdef	72.99 ± 4.55 ab	44.23 ± 8.82 abcde	35.20 ± 9.43 defghij
MEÇ1525.02	89.16 ± 1.64 a	61.92 ± 12.08 abcde	31.43 ± 6.59 efg	36.28 ± 8.55 bcdefghij
MEÇ1525.03	82.85 ± 4.69 ab	53.04 ± 34.55 bcdefg	48.25 ± 4.83 abc	35.95 ± 8.13 cdefghij
MEÇ1525.17	74.06 ± 11.66 abcde	67.36 ± 11.14 abcd	51.44 ± 18.51 ab	46.72 ± 5.58 abcde
MEÇ1530.02	79.87 ± 9.83 ab	64.26 ± 14.24 abcde	44.08 ± 8.34 abcde	29.68 ± 6.48 hij
Agria	57.02 ± 4.32 f	35.44 ± 35.55 fg	28.21 ± 7.13 fg	39.21 ± 7.55 abcdefghi
Desiree	77.03 ± 8.62 abc	64.36 ± 18.93 abcde	24.99 ± 3.07 g	39.73 ± 9.53 abcdefghi
PETEK	68.58 ± 10.57 bcdef	63.22 ± 13.63 abcde	39.88 ± 7.99 bcdef	32.35 ± 8.13 fghij
Russet Burbank	59.93 ± 8.44 ef	32.75 ± 19.61 g	23.97 ± 7.06 g	27.53 ± 8.86 ij
Average	71.95	60.87	40.16	38.23

The first-class tuber distribution values are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

## Discussion

Our study evaluated the agronomic and morphological responses of 29 putative potato genotypes to different temperatures (control temperature; plants received the field temperature of the experimental station, elevated temperature; plants received a temperature of +6.0–10.0 °C), which demonstrated that the growth and productivity of different potato genotypes was affected by

**Table 8** Second-class tuber distribution (%) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.2	25.23 ± 7.95 bcdefg	15.82 ± 7.97 cde	31.58 ± 6.97 cdef	21.66 ± 3.42 fghi
MEÇ1302.15	16.75 ± 2.41 defghi	34.44 ± 22.57 abcd	26.88 ± 9.93 ef	16.92 ± 8.32 hi
MEÇ1302.18	18.56 ± 5.73 cdefghi	30.26 ± 3.98 abcde	35.49 ± 6.42 bcdef	42.62 ± 2.77 a
MEÇ1302.2	20.35 ± 7.45 bcdefghi	17.07 ± 3.58 cde	31.15 ± 4.93 cdef	25.63 ± 5.84 cdefghi
MEÇ1305.05	32.72 ± 6.33 bc	15.83 ± 3.73 cde	35.23 ± 6.46 bcdef	19.25 ± 2.36 ghi
MEÇ1406.07	69.19 ± 30.95 a	44.12 ± 24.64 ab	33.55 ± 5.99 cdef	39.07 ± 5.49 ab
MEÇ1407.05	15.09 ± 6.51 efghi	20.23 ± 9.88 bcde	31.48 ± 10.26 cdef	33.07 ± 10.54 abcdef
MEÇ1407.08	15.69 ± 7.73 defghi	16.33 ± 5.01 cde	43.86 ± 10.65 bc	31.54 ± 7.49 abcdef
MEÇ1407.17	10.33 ± 6.77 hi	19.59 ± 3.97 bcde	34.15 ± 4.84 cdef	35.64 ± 8.61 abcd
MEÇ1409.09	10.36 ± 7.63 ghi	16.15 ± 10.27 cde	29.25 ± 7.13 def	32.87 ± 1.95 abcdef
MEÇ1411.06	15.72 ± 3.44 defghi	24.84 ± 17.49 bcde	36.88 ± 5.53 bcdef	30.49 ± 7.57 bcdefg
MEÇ1501.02	20.65 ± 8.14 bcdefghi	22.19 ± 10.17 bcde	33.73 ± 10.72 cdef	37.12 ± 5.63 abc
MEÇ1502.04	12.87 ± 4.87 fghi	41.39 ± 22.16 abc	30.61 ± 3.35 def	34.52 ± 10.31 abcd
MEÇ1502.15	12.54 ± 2.66 fghi	12.79 ± 10.54 de	28.26 ± 3.69 ef	32.23 ± 6.05 abcdef
MEÇ1502.16	22.81 ± 4.54 bcdefgh	35.21 ± 2.36 abcd	33.48 ± 6.14 cdef	38.85 ± 6.22 ab
MEÇ1502.21	34.12 ± 7.42 b	30.64 ± 10.87 abcd	28.07 ± 6.92 ef	27.38 ± 3.65 bcdefghi
MEÇ1502.25	33.82 ± 16.44 b	23.29 ± 11.36 bcde	37.24 ± 12.94 bcdef	28.68 ± 10.59 bcdefgh
MEÇ1504.01	26.29 ± 9.24 bcdef	13.35 ± 5.09 de	34.96 ± 2.63 cdef	34.32 ± 8.47 abcde
MEÇ1505.02	20.73 ± 7.73 bcdefghi	19.52 ± 12.98 bcde	58.45 ± 9.19 a	29.98 ± 7.28 bcdefg
MEÇ1505.06	25.05 ± 9.11 bcdefgh	26.91 ± 7.92 bcde	42.04 ± 13.22 bcd	35.89 ± 2.93 abcd
MEÇ1505.07	28.65 ± 11.46 bcde	18.53 ± 3.46 bcde	28.79 ± 9.8 ef	32.28 ± 11.48 abcdef
MEÇ1525.02	7.58 ± 1.84 i	15.85 ± 4.53 cde	37.09 ± 11.31 bcdef	34.73 ± 5.97 abcd
MEÇ1525.03	12.45 ± 1.83 fghi	37.11 ± 38.93 abcd	25.33 ± 3.39 f	35.44 ± 6.05 abcd
MEÇ1525.17	20.13 ± 8.09 bcdefghi	4.84 ± 3.86 e	28.72 ± 11.75 ef	25.57 ± 4.72 cdefghi
MEÇ1530.02	17.55 ± 7.87 defghi	13.75 ± 5.74 de	35.83 ± 7.22 bcdef	31.17 ± 6.73 abcdef
Agria	28.89 ± 6.83 bcde	54.82 ± 45.69 a	30.64 ± 10.49 def	22.44 ± 11.94 efghi
Desiree	16.69 ± 4.85 defghi	20.81 ± 11.65 bcde	39.22 ± 5.91 bcde	34.23 ± 4.03 abcde
PETEK	24.62 ± 12.17 bcdefgh	14.13 ± 1.97 de	36.42 ± 3.975 bcdef	24.38 ± 10.55 defghi
Russet Burbank	30.44 ± 4.09 bcd	53.69 ± 26.96 a	47.94 ± 9.2 ab	16.05 ± 13.53 i
Average	22.27	24.60	34.70	30.48

The second-class tuber distribution values are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

temperature. Contrary to many short-term or control conditions heat stress treatments, we applied heat stress from planting to harvest compared with the control conditions under field conditions. Wolf et al. (1990), Lizana et al. (2017), and Mokrani et al. (2023) employed similar stress conditions. Heat-tolerant potato genotypes could be screened by inducing potato genotypes with high temperatures (Khan et al. 2015; Trapero-Mozos et al. 2018) and the tolerance of cultivars

**Table 9** Third-class tuber distribution (%) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.2	1.35 ± 0.87 defg	0.84 ± 0.63 de	17.37 ± 6.12 ij	25.18 ± 7.65 cdef
MEÇ1302.15	1.97 ± 1.04 bcdefg	1.89 ± 2.05 cde	29.19 ± 3.13 bcdef	29.70 ± 19.88 bcde
MEÇ1302.18	1.53 ± 0.94 cdefg	4.62 ± 4.01 abc	34.87 ± 6.63 abc	21.45 ± 8.97 cdef
MEÇ1302.2	0.86 ± 0.52 fg	1.59 ± 0.49 cde	19.37 ± 9.88 fghij	33.29 ± 2.44 bcd
MEÇ1305.05	3.07 ± 2.27 abcd	2.27 ± 1.27 cde	33.65 ± 5.11 abcd	33.99 ± 8.87 bcd
MEÇ1406.07	4.28 ± 0.00 a	3.45 ± 1.37 bcde	38.49 ± 3.93 ab	34.85 ± 8.14 bcd
MEÇ1407.05	0.65 ± 0.64 fg	1.37 ± 0.95 cde	21.38 ± 3.98 efg hij	17.20 ± 14.12 ef
MEÇ1407.08	1.39 ± 0.77 cdefg	0.44 ± 0.41 e	16.98 ± 5.46 ij	26.19 ± 4.74 cdef
MEÇ1407.17	2.38 ± 2.56 abcdef	1.97 ± 0.77 cde	19.16 ± 9.24 fghij	30.12 ± 10.88 bcde
MEÇ1409.09	1.38 ± 1.22 defg	3.95 ± 4.52 bcd	23.95 ± 5.12 defghi	27.86 ± 13.23 bcdef
MEÇ1411.06	0.96 ± 0.61 efg	6.57 ± 5.86 ab	28.56 ± 12.56 bcdefg	21.76 ± 5.89 cdef
MEÇ1501.02	1.04 ± 0.69 efg	1.34 ± 0.76 cde	31.74 ± 9.03 abcde	30.92 ± 8.22 bcde
MEÇ1502.04	0.34 ± 0.09 g	3.16 ± 3.09 bcde	23.14 ± 11.57 defghij	20.46 ± 12.29 def
MEÇ1502.15	0.48 ± 0.29 g	1.99 ± 1.01 de	17.23 ± 2.49 ij	13.48 ± 10.37 f
MEÇ1502.16	2.72 ± 0.93 abcde	8.03 ± 3.49 a	25.75 ± 7.78 cdefghi	24.65 ± 3.56 cdef
MEÇ1502.21	0.86 ± 0.06 fg	2.99 ± 2.76 cde	22.23 ± 6.32 efg hij	23.56 ± 5.37 cdef
MEÇ1502.25	3.42 ± 2.05 ab	2.46 ± 1.01 cde	18.58 ± 8.99 ghij	29.33 ± 11.95 bcde
MEÇ1504.01	1.23 ± 0.59 efg	0.89 ± 0.24 de	13.45 ± 4.96 j	32.27 ± 10.35 bcd
MEÇ1505.02	1.01 ± 0.67 efg	1.54 ± 0.65 cde	17.78 ± 3.05 hij	28.3 ± 3.47 bcdef
MEÇ1505.06	1.54 ± 0.95 cdefg	2.28 ± 1.58 cde	23.75 ± 4.07 defghi	35.37 ± 2.22 bcd
MEÇ1505.07	4.14 ± 1.66 a	1.92 ± 1.15 cde	26.97 ± 3.72 cdefghi	31.37 ± 7.97 bcde
MEÇ1525.02	0.46 ± 0.27 g	3.35 ± 1.53 bcde	31.47 ± 6.97 abcde	26.74 ± 4.35 cdef
MEÇ1525.03	0.89 ± 0.48 fg	1.86 ± 0.00 cde	26.42 ± 4.35 cdefghi	27.33 ± 5.14 cdef
MEÇ1525.17	1.86 ± 1.19 bcdefg	0.51 ± 0.44 de	19.84 ± 9.09 fghij	26.17 ± 8.29 cdef
MEÇ1530.02	1.33 ± 1.05 defg	0.78 ± 0.78 de	20.85 ± 3.53 fghij	35.85 ± 10.23 bc
Agria	3.19 ± 1.12 abc	1.95 ± 0.00 cde	41.14 ± 13.66 a	34.75 ± 13.29 bcd
Desiree	1.57 ± 0.86 cdefg	0.45 ± 0.38 e	35.79 ± 7.76 abc	24.19 ± 9.78 cdef
Petek	1.97 ± 1.62 bcdefg	2.15 ± 2.33 cde	23.69 ± 7.53 defghi	42.75 ± 11.31 ab
Russet Burbank	1.98 ± 1.58 bcdefg	1.55 ± 0.00 cde	28.80 ± 8.45 cdefgh	54.21 ± 7.67 a
Average	1.72	2.35	25.23	29.08

The third-class tuber distribution values are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

evaluated using physiological, biochemical, morphological, and agronomic traits (Rykcaczevska 2015; Kim and Lee 2019; Zhang et al. 2020; Mokrani et al. 2023; Gautam et al. 2024). Previous studies differentially demonstrated that different intensities of heat stress have varied effects on the plant's morphological and agronomic traits (Zhao et al. 2020; Dos Santos et al. 2022).



**Table 10** Malformed tuber distribution (%) in control (CN) and heat (HT) treatments in 2022 and 2023 potato growing seasons

Genotype	2022		2023	
	Control	Heat	Control	Heat
MEÇ1301.2	0±0 b	11.71±9.21 cdefgh	0±0 c	2.79±1.84 c
MEÇ1302.15	0.78±1.26 b	19.26±13.33 abcdef	0±0 c	3.25±1.95 c
MEÇ1302.18	0±0 b	30.49±12.46 a	0±0 c	1.3±0.872 c
MEÇ1302.2	0±0 b	12.18±7.55 cdefgh	0±0 c	1.52±1.87 c
MEÇ1305.05	0.98±1.69 b	12.19±8.11 cdefgh	0±0 c	1.84±2.26 c
MEÇ1406.07	1.13±1.13 b	4.94±4.93 fgh	0±0 c	4.93±2.40 c
MEÇ1407.05	2.40±2.47 b	8.84±6.97 defgh	0±0 c	0.58±1.00 c
MEÇ1407.08	1.27±1.28 b	12.28±10.75 cdefgh	0±0 c	1.74±1.20 c
MEÇ1407.17	5.49±4.69 ab	21.87±14.86 abcde	0±0 c	1.93±1.48 c
MEÇ1409.09	2.95±4.19 b	14.67±15.59 abcdefgh	0±0 c	1.96±0.20 c
MEÇ1411.06	2.97±5.14 b	23.84±14.13 abcde	0±0 c	0.52±0.90 c
MEÇ1501.02	0±0 b	19.39±7.79 abcdef	0±0 c	3.65±1.60 c
MEÇ1502.04	5.86±8.26 ab	24.92±11.46 abc	0±0 c	4.69±3.53 c
MEÇ1502.15	5.68±5.71 ab	13.19±14.49 bcdefgh	0±0 c	1.78±2.00 c
MEÇ1502.16	4.62±1.71 ab	12.57±5.78 bcdefgh	0±0 c	2.17±1.41 c
MEÇ1502.21	3.09±5.36 b	17.95±8.66 abcdefg	0±0 c	0.31±0.54 c
MEÇ1502.25	6.03±1.53 ab	14.17±8.56 bcdefgh	0±0 c	3.48±4.98 c
MEÇ1504.01	1.23±0.76 b	0.89±0.24 h	13.45±1.87 b	32.27±7.77 b
MEÇ1505.02	2.47±4.29 b	12.54±11.64 bcdefgh	0±0 c	3.29±2.45 c
MEÇ1505.06	0.81±0.94 b	8.57±7.02 efgh	0±0 c	0.52±0.89 c
MEÇ1505.07	0±0 b	5.43±3.99 fgh	0±0 c	1.22±0.76 c
MEÇ1525.02	1.83±2.46 b	21.83±12.17 abcde	0±0 c	2.25±1.61 c
MEÇ1525.03	3.35±1.48 ab	9.98±8.38 cdefgh	0±0 c	1.32±1.57 c
MEÇ1525.17	2.67±3.50 b	28.18±12.11 ab	0±0 c	1.53±1.85 c
MEÇ1530.02	0.42±0.73 b	24.64±13.52 abcd	0±0 c	3.29±1.37 c
Agria	5.33±2.69 ab	21.44±6.67 abcde	0±0 c	2.21±2.72 c
Desiree	2.71±2.71 b	19.38±12.44 abcdef	0±0 c	1.85±2.46 c
PETEK	1.97±0.54 b	2.14±0.33 gh	23.69±2.22 a	42.75±9.28 a
Russet Burbank	9.47±3.10 a	3.87±3.36 fgh	0±0 c	4.75±2.59 c
Average	2.68	15.87	1.28	2.21

The malformed tuber distribution (DTY) values are the mean ± standard deviation. Four replicates were averaged and statistically analysed. The means values followed by the same letters in a column are not significantly different ( $P > 0.05$ , Duncan's multiple range test)

Although several studies reported that heat stress impaired potato tuber yield in varying degrees (Rykaczewska 2015; Kim and Lee 2019; Zhang et al. 2020; Gautam et al. 2024), in this study, heat stress generally increased plant height, time to physiological maturity, number of stems per plant, tuber number per plant, total tuber yield, and mean tuber weight with slight variation between seasons. In the first season (S1) of this study, when the mean temperature of the control (CN) condition was around

21.0–23.5 °C, and of the heat stress (HT) around 29.5–31.67 °C, total tuber yield, tuber number per plant (NTP), and mean tuber weight (MTW) of the genotypes significantly increased in the HT compared with the CN, while in the second season (S2), when the mean temperature of the control (CN) was 27.0–29.25 °C and of the heat stress (HT) around 34.0–38.34 °C, no significant variation in the TTY, MTY, NTP, and MTW was observed. Gautam et al. (2024) stated that temperatures ranging within 12–28 °C are favourable ranges for higher potato yields, this somehow aligns with the 27 to 33 °C found in this study. Lizana et al. (2017) and Wolf et al. (1990) found increased tuber yield and number of tubers per plant of potato varieties when exposed to higher temperatures under field conditions. Similar results of an increase in potato tuber yield, and mean tuber weight were observed by Mokrani et al. (2023) when assessing the effect of temperature on tuber production and carbohydrate partitioning in potatoes; however, their reduced number of tubers per plant contradicts the current study. A drastic reduction in potato yield was observed by Rykaczewska (2015), Kim and Lee (2019), and Zhang et al. (2020) under heat stress in both control and field conditions. These contradictions could be due to differences in cultivar, experimental conditions, and seasonal changes. In this study, the 2022 season was characterised by low temperatures and high relative humidity while the 2023 season was characterised by high temperature and low relative humidity. This combination of weather conditions could have favoured the high yield in 2022; however, the weather conditions in 2023 could have created unfavourable conditions resulting in a generally low yield and relatively high morphological traits. This aligns with the significant potato yield variations under varying weather conditions (Lee et al. 2020) that changes in climatic conditions could either promote or inhibit tuber yield and quality of potatoes (Gautam et al. 2024).

In both seasons, elevated temperature caused an increase in plant height, physiological maturity time, and the number of stems per plant that could be attributed to rapid growth as supported by Siano et al. (2024), heat stress increased plant height and leaf area because of rapid growth. The tuber yield contradiction of this study with the several studies could also be due to differences in the genotype's response to heat stress and the treatment. Most heat stress studies on potatoes have been done under control conditions (Tang et al. 2018; Lee et al. 2020; Zhang et al. 2024), in which high temperatures caused decreased tuber yield. This could be due to differences in genotypes. The high TTY, NTP, and MTW are buttressed by Siano et al. (2024) who observed high yield in potatoes in a multi-environmental assessment of the impact of heat stress on potato growth and development while contradicting the 13% (Patino-Torres et al. 2021), 4.5 to 34.8% (Mahmud et al. 2021), 67% (Gautam et al. 2024) of yield reduction. The 2022 season produced a higher number of larger tubers compared to the 2023 season while the 2023 season produced a higher number of tubers per plant compared with the 2022 season. The observations of the high number of tubers per plant in this study contradict the decreased formation of tuber number per plant (Zhang et al. 2021) while aligning with the numerous smaller tubers (Mahmud et al. 2021; Gautam et al. 2024) observed in the 2023 season due to delay in tuber initiation due to heat stress as the 2023 season recorded higher temperatures than the 2022 season for both control and heat treatments. Also, the higher number of tubers in 2023 could have resulted in smaller tuber sizes due to strong competition for

assimilates partitioned to the tubers. Thus, heat stress could either reduce the average number of tubers per plant or increase the number of tubers per plant based on the severity, timing of heat stress, and genotypic differences for time to tuber initiation of different genotypes (Gautam et al. 2024).

Cultivar, season, and their interaction jointly dictate yield capacity (Benavides-Cardona et al. 2022), and tuber size distribution with the season significantly impacting yield, tuber size distribution, and percentage of malformed tubers. Heat stress had a different and significant impact on the tuber size distribution and malformation of the potato genotypes, resulting in the reduction in marketable tuber yield of the heat stress compared to the control although the heat stress conditions generally had higher total tuber yield than the control. Also, cultivar plays a role in tuber malformation which explains their susceptibility levels to heat stress as was found in this study. Potato cultivars with naturally large and elongated tubers are more susceptible to malformation while cultivars with medium-sized circular tubers are less susceptible to malformation but more susceptible to growth cracks (Siano et al. 2024). Siano et al. 2024 found that the development of a specific tuber physiological disorder in potatoes depends on the environment and the specific (or combination of) abiotic stress present during the growing season. In arid conditions, combined heat and drought stress results in second-growth formation such as heat sprouts, chain tubers, and secondary tuber formation (Zhang et al. 2021). This could explain the highly significant number of malformed tubers in the heat stress conditions compared with the control as influenced by elevated temperature and season.

Periods and duration of heat stress application play an important role in potato yield response (Wolf et al. 1990; Kim and Lee 2019; Lee et al. 2020). Plant exposure to a longer period of heat stress confers heat stress tolerance (Wolf et al. 1990). Studies report that heat stress during the tuber bulking stage has no adverse effect on the tuber yield; however, an increase in temperature for 20 days at the onset of tuber bulking effectively increases the tuber yield of potatoes (Lizana et al. 2017). In this study, the heat stress was applied from the onset of the experiment, this could have conferred stress adaptive mechanisms of the potato genotypes. Also, the observed yield results in this study could be due to the corresponding increase in CO<sub>2</sub> as temperature increased. Concurrent elevation of temperature and CO<sub>2</sub> within the effective range will exert positive effects on the growth, yield, and photosynthesis of potato crops (Lee et al. 2020) leading to vigorous canopy development that results in enhanced interception of solar radiation.

## Conclusion

Heat stress threatens potato production in many regions of the world, and the development of heat-tolerant potato cultivars is needed globally for food sustainability. The impact of elevated temperature on the morphological and agronomic traits was evaluated in this study under field conditions. Plant height, days to physiological maturity, and number of stems per plant were significantly increased under elevated temperatures. These traits can serve as morphological

traits for selecting heat-tolerant potato lines. Elevated temperatures around 27.0 to 33.0 °C significantly promoted tuber yield, tuber number per plant, and mean tuber weight compared with temperatures around 20.0 to 24.0 °C but caused no significant effect at 34.0 to 38.0 °C temperature ranges. The tuber size distribution was affected by the range of temperature increase. Temperatures from 27 °C to 33 °C increased the percentage of first and second-grade tubers and the weight of tubers. This may be attributed to an acclimation response to potato to heat stress. Our study demonstrated that the time of heat stress application plays a vital role in determining the heat tolerance capacity of potatoes. In potatoes, elevated temperatures up to 33.0 °C from the onset of planting to harvest confer heat stress tolerance and increase yield and yield-related traits. Thus, the elevation of temperature within the effective range will exert positive effects on the yield, and yield-related components of potato crops.

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## Declarations

**Conflict of Interest** The authors declare no competing interests.

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