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Response of Tomato Quality and Yield to Elevated Temperatures under Controlled Environment

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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ABSTRACT

The experiment was carried out during 2020-2021 at the Department of Plant Physiology, College of Agriculture, Vellayani, Kerala Agricultural University. The experiment was carried out with the aim of characterization of contrasting tomato genotypes for high temperature tolerance under high temperature condition and control condition to identify key quality and yield traits controlling high temperature tolerance in tomato. The experiment was designed in completely randomized design (CRD) with 2 treatment levels- control and high temperature conditions (36+/-2^{o}C) wherein 3 tolerant and 3 susceptible genotypes were selected for the study. These genotypes were selected from the summer varietal screening experiment performed during the summer months of 2021 from March to May. The best performing genotypes were selected in terms of pollen viability, leaf membrane thermo-stability, chlorophyll fluorescence, number of fruits, fruit set %. One set of treatment was maintained under ambient condition and the other set with high temperature stress was maintained under polyhouse facility from transplanting stage to the harvesting stage. The quality parameters and yield traits were analysed at the harvesting stage of the crop. From this study it can be understood that many of the quality parameters like lycopene content, total sugars,

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flavanol content was found decreasing in both tolerant and susceptible genotypes but the extend of this reduction was considerate in tolerant ones. In case of ascorbic acid content and firmness of fruit at the time of ripening these were found to be improved in heat stress (HS) conditions. Yield related qualities like number of fruits, yield per plant, and root-shoot ratio was found decreasing whereas root dry weight, total dry weight and intensity of fruit drop and flower drop was increased under HS. Therefore, this study focused on tomato genotypes reported to be resilient to high-temperature stress, and comparing them to the susceptible cultivars under stress and control settings for analyzing the variations in terms of quality and yield traits in tropical hot climate regions of India. The study performed here highlights the possibility for future breeding programs utilizing the key quality and yield traits enhancing thermo-tolerance in tomato and to develop new genotypes that can combine good yield performances and fruit nutritional quality at high temperatures.

Keywords: Antioxidant; heat stress; quality; tomato; yield.

1. INTRODUCTION

It is anticipated that one of the industries negatively impacted by climate change will be agriculture, and that effect will become more noticeable in the coming years [1]. One of the effects of global climate change that may have a significant impact on the quantity and quality of horticulture crops is rising air temperatures [2]. Tomato is one of the products that has a large consumption and cultivation area in the world. High temperature is significant environmental stress that limits plant growth and agricultural productivity. Moreover, the tomato is one of the primary species that is highly susceptible to elevated temperatures. Optimum temperatures for the development of flower organs, pollen, and fruit sets are between 15 and 32 ° C, and temperatures of 35 °C and above directly distress vegetative and generative development. Moreover, tomato fruit has a wealth of vital elements, including minerals like calcium, phosphorus, iron, phenols, flavones, carotenoids, vitamin C, vitamin A, and strong antioxidants [3,4].

Lycopene is the compound that gives tomatoes their red color—protects human health in a number of ways. Elevated temperatures pose a substantial environmental strain on plant development and agricultural output. One of the main species that is particularly vulnerable to high temperatures is the tomato. Temperatures of 35°C and above immediately disrupt vegetative and generative development [5]. The ideal range for the development of flower organs, pollen, and fruit sets is between 15 and 32°C [6,7]. The fluctuations in temperature disrupt the morphology, anatomy, phenology, and biochemistry of plants at every level of organization [8]. In particular, high temperatures stress tomatoes, causing blossom abortion and limiting fruit set that results in significant yield losses [9]. Increased temperature can also affect the quality and nutritional qualities of tomatoes, as well as their physical characteristics (size, color, etc.) [10].

Plant morphology, anatomy, phenology, and biochemistry are all disrupted by temperature variations at all organizational levels. Elevated temperatures directly result in protein denaturation, which in turn causes membrane lipids to become more fluid, enzymes in mitochondria and chloroplasts to become inactive, and membrane integrity to be disrupted in plants [11]. Furthermore, plants under high temperature stress produce reactive oxygen species (ROS) like hydrogen peroxide, singlet oxygen, superoxide, and hydroxyl radicals; the accumulation of ROS is the main cause of crop loss [8,12,13]. It was discovered that when tomatoes experienced stress, their stomata closed, increasing the leaf's temperature and reducing photosynthesis [14]. In a similar vein, it was shown that stomata reopened as the temperature of the leaves decreased, and plants proceeded to grow by carrying out photosynthesis as usual in these circumstances [15,16]. Moreover, high temperatures in the greenhouse decreased photosynthesis and tomato yield, according to Zhang et al. [17]. Zhang et al. [18] reported that in plants exposed to 35°C, stomatal conductivity, intercellular CO2 concentration, and transpiration rate rose, but net photosynthesis rates decreased in comparison to the control group [19]. Furthermore, since a larger total number of leaves and, thus, a greater surface area would result in a more substantial amount of water lost by transpiration, declines in the number of leaves are likely to be noticed due to delayed plant growth in high-temperature stress circumstances [20]. Finally, it was underlined that when plants are stressed by high

temperatures, they attempt to minimize transpiration by contracting the area of their leaves, which closes their stomata as much as possible [15]. Raising the temperature from 27°C to 32°C results in lower ascorbate and lycopene concentrations, but higher glucoside and regular caffeic acid derivative contents [18]. During fruit development, temperature affects assimilation, transport, and storage. During the phases of fruit ripening, structural and functional molecules including starch and secondary metabolites that affect the interior quality are created [20]. The assimilation of photosynthetic processes in the leaves results in the dry matter of the fruit, which is subsequently transferred to the fruit as sucrose. The flavor of tomatoes is determined by the transformation of sucrose and other sugars into organic acids and fragrance compounds [21]. Fruit quality is also influenced by environmental factors like as temperature, water irradiation, and photosynthesis [22]. While numerous studies have been conducted on the physiology, plant growth, and yield of tomatoes grown in high temperatures but few studies have been done on how high temperatures alter the fruit's antioxidant and nutrient content. In this context, there is necessity for conducting experiments.

Conducting experiments to study the response of tomato quality and yield to elevated temperatures under controlled environments is crucial for understanding the impact of heat stress on tomato plants. These experiments involve subjecting tomato plants to specific temperature conditions, such as ambient day/night temperatures that exceed 32°C/20°C, which are known to negatively affect fruit set, fruit weight, and overall yield. By comparing different tomato genotypes or cultivars, researchers can identify heat-sensitive and heat-tolerant varieties, as well as determine the physiological and biochemical changes that occur in response to heat stress. The findings from these experiments can contribute to the development of thermotolerant tomato cultivars that can withstand high temperatures and maintain high fruit yield and quality, even under heat stress conditions.

2. MATERIAL AND METHODS

Three tolerant and three susceptible genotypes were selected based on the summer varietal screening performed during the summer season from March to May, 2022. the best performing genotypes in terms of pollen viability, leaf membrane thermo-stability, chlorophyll fluorescence, number of fruits, fruit set % (Table 1). The aim of this experiment was to determine the critical quality and yield characteristics regulating high-temperature tolerance in different tomato genotypes under high-temperature circumstances.

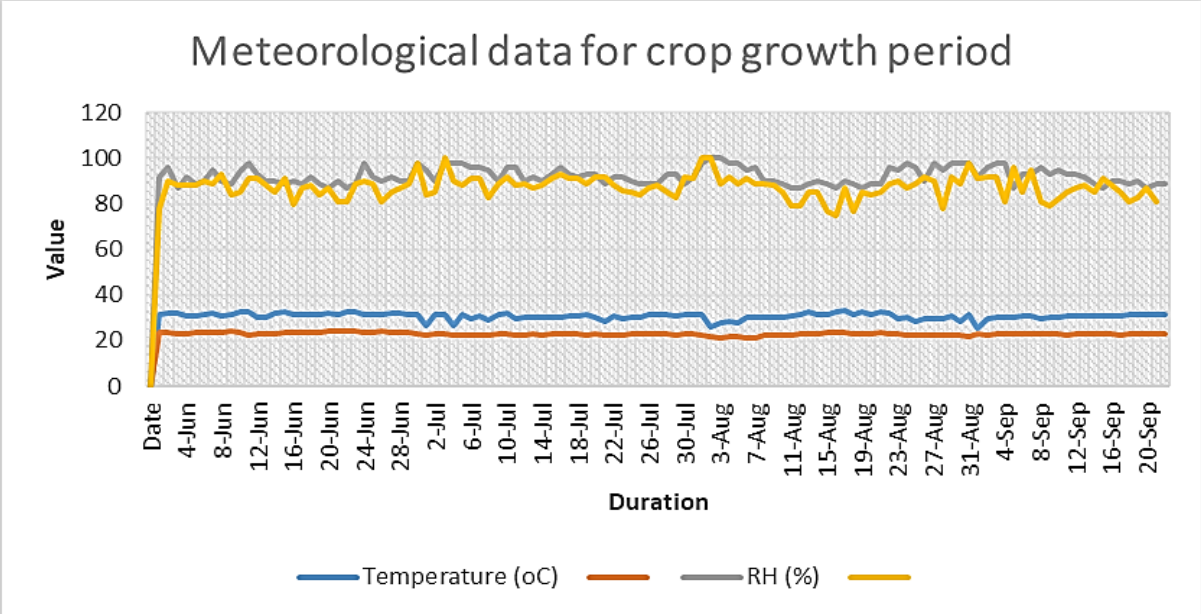

Fig. 1. Meteorological data during crop growth period including temperature (^{O}C) and RH (%)

Table 1. Range, mean, standard deviation of various traits of tomato genotypes under high-temperature condition during summer months of 2022

Sl. No	Variables	Maximum	Minimum	Mean	S.E	C.D
1	Photosynthetic rate (PR)	Anagha (22.9µmol CO2 m-2 s-1)	EC-313466 (11.28µmol CO2 m-2 s-1)	15.56	1.01	2.15
2	Stomatal conductance (SC)	Marutham (68mol H_2O m^{-2} s^{-1})	Kashi Vishesh (32mol H_2O m^{-2} s^{-1})	47.45	3.39	7.18
3	Pollen viability (PV)	Anagha (98.20%)	Arka Vikas (53.26%)	73.44	1.23	2.61
4	Chlorophyll fluorescence (CF)	Arka Sourabh (0.78)	Vellayani Vijay (0.48)	0.65	0.05	0.11
5	Chlorophyll content (CHL)	Vellayani Vijay (2.68 mg g^{-1} FW)	Pusa Rohini (0.74mg g^{-1} FW)	1.24	0.20	0.42
6	Leaf membrane thermostability (LMT)	Anagha (78.48%)	Pusa Rohini (30.48%)	53.38	1.10	2.23
7	Number of fruits	Kashi Vishesh (59)	Arka Sourabh (4)	20.15	7.38	15.64
8	Fruit set %	Vellayani Vijay (91.41%)	PKM-1 (2.33%)	18.94	5.57	11.80
9	Yield per plant	Vellayani Vijay (1146.09 g)	IC-45 (2.3g)	18.42	2.85	6.03

The experiment was set up using a completely randomized design (CRD), with three replications of each of the two treatment levels-control and high-temperature stress with a temperature range of 36 +/- 2°C. With proper labelling, seeds were planted in pots filled with potting soil (a 2:1 blend of vermicompost and coir pith compost). Regular irrigation was offered. After thirty days of germination, seedlings were transplanted into pots filled with potting mixture comprised of equal parts soil, sand, and cow dung. Throughout the experiment, a digital thermo-hygrometer was used to record the daily temperatures, including the highest and lowest temperatures as well as the relative humidity levels under both control and heat stress circumstances (Fig. 1) represent weather data for kharif season both under control and heat stress conditions respectively. From transplanting till harvesting, one treatment group was kept in ambient conditions, and the other group, which was subjected to severe temperature stress, was kept in a polyhouse facility. The crop was grown in accordance with Package of Practices (POP) recommendations. The observations were made at the appropriate stage.

2.1 Invertase Enzyme Activity

Five ripened fruits were picked randomly from each treatment to determine the following quality parameters. Invertase enzyme activity was determined as described by [23,24]. In a reaction mixture comprising 1.5 ml of the enzyme extract and 0.2 ml of 20 mM sucrose mixed in 100 mM acetate buffer (pH 4.7), the activity of soluble acid invertase was examined. At 30°C, the mixture was incubated for 30 minutes. Test tubes were submerged in a bath of hot water for three minutes in order to stop the reaction. The boiling-inactivated enzyme preparation was present in the control sample. The amount of free fructose in the mixture was used to calculate the amount of hydrolyzed sucrose.

2.2 Total Flavanol Content (mg g-1 FW)

According to Fukumoto and Mazza [25], the total flavonoids were calculated and the absorbance at 510 nm was measured by means of a spectrophotometer and quercetin as standard. The method consisted of mixing 0.25 mL of sample with 0.25mL of 0.1% HCl in 95% ethanol and 4.55 mL of 2% HCl. The absorbance of the solution was then read at 360 nm to measure flavonols. Standard used was quercetin for flavonols. Standards were prepared in 100% methanol.

2.3 Total Sugar Content (mg g-1 FW)

The Anthrone technique was used to determine the total soluble sugar concentration [26]. In a mortar, 0.5 g of the fresh leaf was crushed, and 5 ml of 80% hot alcohol was added. The mixture was centrifuged for 15 minutes at 6000 rpm at 9000 g. After the resulting supernatant was separated, 12.5 ml of 80% alcohol was added to another test tube. After taking 1 milliliter of the solution, 1 milliliter of 0.2% anthrone was added. For ten minutes, the mixture was heated to 100°C in a waterbath. The mixture was allowed to sit on ice for five minutes in order to stop the reaction. The amount of total soluble sugar was calculated at 620 nm using a spectrophotometer. Calculation of the total soluble sugar content was done by creating a standard curve using a standard glucose and was expressed in mg/g fresh weight.

2.4 Ascorbic Acid Content (mg g-1 FW)

By using the 2,6-dichlorophenol indophenol (DCPIP) AOAC technique (967.21), the ascorbic acid concentration was determined [27]. After thoroughly mixing ten grams of tomato puree with a 4% oxalic acid solution and pressing the mixture through a muslin cloth, the volume was increased to fifty milliliters. Titrating a known amount of the extract against DCPIP allowed for the estimation of the ascorbic acid level. Using a standard curve of L-ascorbic acid, ascorbic acid concentration was determined as mg of ascorbic acid equivalents per 100 g of fruit fresh mass (FFM).

2.5 Lycopene Content (mg g^{-1} FW)

Lycopene was estimated as previously described by Fish et al. [28]. 50 mg of ground frozen fruit were extracted with 250 µL of MiliQ water, 450 µL of acetone, 450 µL of ethanol and 675 µL of n-hexane. The apolar phase was recovered and the rest was re-extracted with 675 µL of n-hexane. The recovered phases were combined, and the absorbance was read at 503 nm and 800 nm with quartz microplates.

2.6 Yield Related Observations

At regular intervals beginning with the initiation of flowering, the number of fruits per plant was counted on five plants in each treatment. Combining the quantity of fruits and fruit mass that were regularly picked allowed researchers to calculate the yield per plant (g) and number of fruits per plant in the same plants. Data on the

fruit drop were recorded under each treatment from the date of fruit setting till the time of fruit harvesting. The percentage of fruit drop under each treatment was calculated by dividing the number of fruits dropped to total number of fruits obtained from each replication within a treatment.

For biomass measurements, leaves and stems were processed separately. After that, plant tissues were dried in an oven for 1week at 65°C and weighed to quantify the root dry weight (DW). Weight was taken for the root portion and shoot portion separately and the we obtain the total dry weight by adding up both the weights and is given in g. For analyzing the root-shoot ratio (R:S ratio), the root dry weight is divided by the shoot dry weight.

2.7 Statistical Analysis

An ANOVA was performed on the collected data to ascertain the statistical significance among the different genotypes. The results were assessed using the two-factor analysis and replications using the GRAPES software. We computed the means and standard errors. The data were subjected to a one-way analysis of variance (ANOVA) at a significance threshold of $p \leq 0.05$ using GRAPES software. Duncan's multiple range test was used to compare the mean values when the ANOVA findings were significant.

3. RESULTS

The two sets of treatment, i.e. plants grown in the control and high temperature stress conditions is given in Fig. 2. All the genotypes under study showed an increase in the content of ascorbic acid in the plants when compared to the control plants (Table 2). Highest ascorbic acid content was observed in Vellayani Vijay (27.57 mg g^{-1} fresh weight) under control conditions whereas it was maximum for Kashi Vishesh (32.48 mg g^{-1} fresh weight) under HS conditions. In the case of lowest rates of ascorbic acid produced in the fruit, under both the conditions it was for Arka Vikas which were 10.06 mg g^{-1} fresh weight and 10.43 mg g^{-1} fresh weight for control and HS conditions respectively. Both genotypes, Vellayani Vijay and Kashi Vishesh were on par in terms of the ascorbic acid content produced under both growing conditions.

Fig. 2. a) Overview of tomato plants in polyhouse (high temperature condition)

Fig. 2. b). Overview of tomato plants in control condition (60 DAS)

Table 2. Effect of heat stress on ascorbic acid content in different tomato genotypes expressed in mg g-1 FW

Genotypes	Ascorbic acid (mg g-1 FW)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	27.53[c]	32.48[a]	30.01[a]
Vellayani Vijay (T2)	27.57[c]	30.47[b]	29.02[a]
Anagha (T3)	21.96[e]	25.47[d]	23.72[b]
Pusa Rohini (T4)	14.87[f]	15.87[f]	15.37[c]
PKM-1 (T5)	12.10[g]	12.86[g]	12.48[d]
Arka Vikas (T6)	10.06[h]	10.43[h]	10.24[e]
Mean (D)	19.02	21.26	
C.D.(p≤0.05)	P=1.143, D=0.66, P×D=1.617		
SE(m)	0.554		
CV	4.763		

Table 3. Effect of heat stress on invertase enzyme activity in different tomato genotypes expressed in mg Glu h-1 mg-1 protein

Genotypes	Invertase activity (mg glucose released $h^{-1}mg^{-1}$protein)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	0.77	0.68	0.73[a]
Vellayani Vijay (T2)	0.80	0.73	0.76[a]
Anagha (T3)	0.69	0.61	0.65[a]
Pusa Rohini (T4)	0.56	0.45	0.50[b]
PKM-1 (T5)	0.52	0.43	0.48[c]
Arka Vikas (T6)	0.44	0.32	0.38[d]
Mean (D)	0.63[a]	0.54[b]	
C.D.(p≤0.05)	P=0.036, D=0.021, P×D=18.76		
SE(m)	0.017		
CV	5.182		

Vellayani Vijay showed the highest value of invertase activity in both control and HS conditions, measuring 0.80 mg of glucose released h-1mg-1 protein and 0.73 mg of glucose released h-1mg-1 protein, respectively, while Arka Vikas showed the lowest value, measuring 0.44 mg of glucose released h-1mg-1 protein and 0.32 mg of glucose released h-1mg-1 protein, under both conditions. The percentage decrease in SPS was approximately 3-7% for genotypes that were tolerant and 11–13% for those that were susceptible. The mean value was 0.63 mg of glucose released h-1mg-1protein under control conditions and 0.54 mg under high-stress conditions (Table 3).

Vellayani Vijay had the highest flavanol content in both control and HS conditions, measuring 10.94 mg g-1 fresh weight and 12.37 mg g-1 fresh weight, respectively, while Arka Vikas had the lowest flavanol content in both conditions, measuring 5.12 mg g-1 fresh weight and 6.94 mg g-1 fresh weight, respectively. Under stressful situations, it was discovered that the flavanol content increased. This rise was lowest for Vellayani Vijay (1.03%) and largest for Arka Vikas (3.54%), who had the susceptible and tolerant genotypes, respectively (Fig. 3). In tolerant genotypes, the percentage increase in flavanol content was approximately 1-2%, while in sensitive genotypes, it was approximately 2-4% (Fig. 3).

It was discovered that when genotypes are produced under heat stress, the total sugar content drastically decreases (Fig. 3). The research genotypes differed in the rate at which the total sugar concentration decreased. Kashi Vishesh had the lowest percentage rate of reduction (23.4%), while Arka Vikas had the highest (29.25%). Vellayani Vijay and Arka Vikas had the greatest and lowest rates of total sugar content for both situations; under control, the values were 3.01 mg g-1 FW and 1.89 mg g-1 FW, while under stress, the values were 2.19 mg g-1 FW and 1.34 mg g-1 FW. In genotypes that are tolerant to heat stress, total sugars were observed to decrease by 23–30%, while in susceptible genotypes, the rate of reduction was 29–37%.

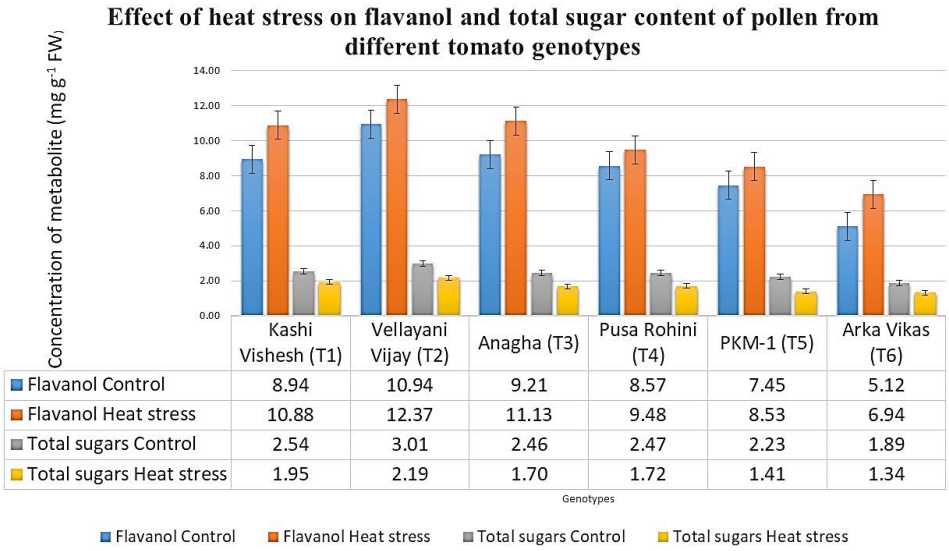

Fig. 3. Effect of heat stress on flavanol and total sugar content of pollen from different tomato genotypes

Lycopene content was found decreasing in both tolerant and susceptible genotypes when plants were grown under high temperature conditions when compared to control (Table 4). Under control as well as HS conditions the highest value of lycopene content was recorded in Vellayani Vijay with values of 13.88 mg g-1 FW and 12.73 mg g-1 FW respectively whereas, it was lowest in case of Arka Vikas under control and HS condition with value of 5.51 mg g-1 FW and 4.32 mg g-1 FW respectively.

The intensity of fruit drop was highest for Arka Vikas (57.87%) and lowest for Anagha (14.53%) in control treatment and in HS it was maximum for Arka Vikas (41.34%) and minimum for Kashi Vishesh (6.32%). Only resistant variety fruited at significant quantities, while sensitive kinds produced minute, deformed fruits with lowest fruit drop and maximal blossom drop. Treatments revealed considerable variance for fruit drop severity, however genotype and temperature regime interactions and variety exhibited non-significant variation (Table 5).

In comparison to the control temperature, all genotypes showed a considerable drop in the number of fruits per plant at high temperatures. Vellayani Vijay (64.67) produced the most fruits, whereas Arka Vikas (11.33) produced the fewest under control circumstances. But Kashi Vishesh (50.67) produces the most fruits under heat stress, whereas Arka Vikas (4.33) produces the fewest. The tolerant genotypes showed the least percent drop in fruit yield per plant, ranging from 30 to 40%, while the susceptible genotypes showed the most percent decrease, ranging from 80 to 98% (Table 6).

All tomato genotypes showed a significant loss in yield per plant at high temperatures in comparison to the control temperature. Heat-susceptible genotypes showed yield reductions of 80–90% whereas susceptible genotypes showed yield reductions of 25–40% under heat stress conditions (Table 9). Arka Vikas produced lowest rate for yield per plant under both temperature conditions, 418.13g under control and 48.25g under stress, whereas Vellayani Vijay produced higher yield in both HS and control conditions, 2952.06g and 2068.44g, respectively. Only genotypes that are tolerant in nature yielded larger fruit yields per plant than the susceptible ones (Table 7).

Genotypes like Kashi Vishesh, Anagha, PKM-1and Arka Vikas were on par under control conditions whereas Kashi Vishesh and Pusa Rohini under study were significantly on par under HS conditions. Mean value of root dry mass was 0.76g and 1.87g for control and HS conditions respectively. Highest values of R:S ratio for control and HS conditions was observed in Pusa Rohini (1.40g) and Anagha (2.60g) respectively whereas lowest values were observed in Velayani Vijay under both conditions which was 0.31g and 1.29g respectively (Table 9).

Table 4. Effect of heat stress on lycopene content in different tomato genotypes expressed in mg g-1 FW

Genotypes	Lycopene (mg g-1 FW)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	9.80^{c}	8.65^{b}	9.23^{b}
Vellayani Vijay (T2)	13.88^{a}	12.73^{a}	13.31^{a}
Anagha (T3)	10.10^{b}	8.06^{c}	9.08^{c}
Pusa Rohini (T4)	9.80^{c}	5.08^{d}	7.44^{d}
PKM-1 (T5)	8.97^{d}	4.96^{e}	6.96^{e}
Arka Vikas (T6)	5.51^{e}	4.32^{f}	4.92^{f}
Mean (D)	9.68^{a}	7.30^{b}	
C.D.(p≤0.05)	P=0.709, D=0.409, P×D=1.003		
SE(m)	0.344		
CV	7.011		

Table 5. Effect of heat stress on the intensity of fruit drop in different tomato genotypes expressed in %

Genotypes	Intensity of fruit drop (%)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	6.32	16.72	11.52^{c}
Vellayani Vijay (T2)	7.57	15.73	11.65^{c}
Anagha (T3)	8.40	14.53	11.46^{c}
Pusa Rohini (T4)	29.58	42.09	35.84^{b}
PKM-1 (T5)	27.12	45.40	36.26^{b}
Arka Vikas (T6)	41.34	57.87	49.60^{a}
Mean (D)	20.06^{b}	32.06^{a}	
C.D.(p≤0.05)	P=5.313, D=3.067, P×D=N.A.		
SE(m)	2.574		
CV	17.112		

Table 6. Effect of heat stress on number of fruits per plant (NFP) in different tomato genotypes expressed in numbers

Genotypes	NFP		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	64.00^{a}	50.67^{b}	57.33^{a}
Vellayani Vijay (T2)	64.67^{a}	45.33^{c}	55.00^{a}
Anagha (T3)	54.00^{b}	35.67^{d}	44.83^{b}
Pusa Rohini (T4)	22.67^{e}	8.33^{gh}	15.50^{c}
PKM-1 (T5)	15.33^{f}	7.33^{gh}	11.33^{d}
Arka Vikas (T6)	11.33^{fg}	4.33^{h}	7.83^{e}
Mean (D)	38.67^{a}	25.28^{b}	
C.D.(p≤0.05)	P=3.411, D=1.969, P×D=4.824		
SE(m)	1.653		
CV	8.953		

Plant height and weight per stem showed a significant increase under high CO2 conditions (570 µmol mol-1). It has been shown that plants cultivated in polyhouses with high temperatures develop tall root systems that enable them to adapt and survive under stressful circumstances. The result shows that the average root-shoot ratio under stress circumstances was 0.69, and under control it was 0.41. Grown under both settings, genotypes Kashi Vishesh and Vellayani Vijay were shown to perform similarly in terms of R:S ratio, whereas PKM-1 and Pusa Rohini were equally comparable under control conditions. Arka Vikas (0.61) and Pusa Rohini (0.89) showed the maximum R:S ratio under control and HS, while Vellayani Vijay (0.32) and Kashi Vishesh (0.89) showed the lowest (Table 8).

Table 7. Effect of heat stress on yield per plant in different tomato genotypes expressed in g

Genotypes	Yield per plant (g)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	2851.06^{a}	1791.16^{c}	2321.11^{a}
Vellayani Vijay (T2)	2952.06^{b}	2068.44^{d}	2510.25^{b}
Anagha (T3)	2537.59^{b}	1541.47^{cd}	2039.53^{b}
Pusa Rohini (T4)	996.99^{e}	399.58^{f}	698.29^{c}
PKM-1 (T5)	755.06^{e}	204.11^{fg}	479.59^{d}
Arka Vikas (T6)	418.13^{f}	48.25^{g}	233.19^{e}
Mean (D)	1647.31^{a}	913.34^{b}	
C.D.(p≤0.05)	P=203.837, D=117.685, P×D=288.268		
SE(m)	98.763		
CV	13.361		

Table 8. Effect of heat stress on root-shoot ratio in different tomato genotypes

Genotypes	R:S Ratio		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	0.33^{fg}	0.55^{de}	0.44^{d}
Vellayani Vijay (T2)	0.32^{fg}	0.62^{de}	0.47^{d}
Anagha (T3)	0.45^{ef}	0.80^{ab}	0.63^{ab}
Pusa Rohini (T4)	0.52^{de}	0.89^{cd}	0.59^{bc}
PKM-1 (T5)	0.55^{de}	0.62^{a}	0.70^{a}
Arka Vikas (T6)	0.61^{g}	0.70^{bc}	0.50^{cd}
Mean (D)	0.41^{b}	0.69^{a}	
C.D.(p≤0.05)	P=0.099, D=0.057, P×D=0.14		
SE(m)	0.048		
CV	14.955		

Table 9. Effect of heat stress on root dry weight in different tomato genotypes

Genotypes	Root DW (g)		
	Control (C)	Stress (H)	MEAN (P)
Kashi Vishesh (T1)	0.59^{e}	1.72^{c}	1.16^{c}
Vellayani Vijay (T2)	0.31^{f}	1.29^{d}	0.80^{d}
Anagha (T3)	0.87^{e}	2.60^{a}	1.74^{a}
Pusa Rohini (T4)	1.40^{d}	1.72^{c}	1.56^{ab}
PKM-1 (T5)	0.66^{e}	1.56^{cd}	1.11^{c}
Arka Vikas (T6)	0.77^{e}	2.32^{b}	1.53^{b}
Mean (D)	0.76^{b}	1.87^{a}	
C.D.(p≤0.05)	P=0.198, D=0.114, P×D=0.28		
SE(m)	0.096		
CV	12.634		

4. DISCUSSION

One of the biggest obstacles to crop production is HS, which negatively impacts the tomato plant's vegetative and reproductive processes and eventually lowers fruit quality and yield [29]. Furthermore, some justifications have been put forth regarding why tomatoes don't reproduce well in hot climates. These consist of low or aberrant amounts of carbohydrate, low levels of pollen, aberrant development of the female reproductive tissues, hormonal abnormalities, and lack of pollination [30,31]. According to Guichard et al. [32], high temperatures in tomato plants have an impact on a number of physiological and biochemical processes that ultimately lead to a decrease in production. The following biological and/or physiological processes may be impacted by temperature: stomatal conductance to CO2 diffusion and photoassimilate translocation; photosynthetic enzyme activity; membrane integrity;

photophosphorylation; and electron transport in chloroplasts [33,34,35].

High temperatures negatively impact tomato plants during their vegetative and reproductive stages, which lowers fruit quality and yield [36]. Due to a disrupted root-nutrient interaction, high temperatures exacerbate root heat stress (HS) and have an adverse effect on nutritional quality [37,38]. Thus, by restricting the availability of water, nutrients, and hormones that affect the sink-source relationships between roots and shoots, high temperatures inhibit root growth, diminish the shoot system, and ultimately lower fruit output [39,40]. Decreases in nutrient acquisition with heat stress could potentially be caused by several factors, including a decrease in root mass or surface area and/or a decrease in nutrient uptake per unit root, as well as reduced photosynthetic efficiency [39]. Furthermore, it is evident that reductions in root growth and the rate at which plants absorb nutrients are the result of heat-stress-induced cell damage in the root [40]. This damage ultimately leads to a decline in root growth and the overall concentration of proteins, including a decrease in the levels of proteins responsible for nutrient uptake, and potentially affects the activity of specific uptake proteins, such as their transport or reaction rates [42]. All these results were on par with the results obtained from our results and they ultimately resulted in reduced crop quality and yield.

Pigments called chlorophylls are necessary for photosynthesis. There may be instances where a lower chlorophyll content has no effect on photosynthesis, but generally speaking, the higher the chlorophyll content, the faster the rate of photosynthesis [41,42]. During fruit development, temperature affects assimilation, transport, and storage. Lower night temperature interferes in starch accumulation before anthesis by decreasing the concentration of soluble sugar in mature pollen grains [43]. Whereas, when plants grown at high day temperature along with low night temperature, there will be 50% reduction in enzyme activities of pollen cell wall and soluble acid invertase that catalyze the hydrolysis of sucrose [44,45].

According to reports, raising the temperature in tomato cultivation from 21°C to 26°C during night time lowers the total carotene content but has no effect on the lycopene content; conversely, raising the temperature from 27°C to 32°C lowers the ascorbate and lycopene content while increasing the glucoside and routine caffeic acid derivatives contents [46,47]. Genotypes which are tolerant in nature in high temperatures, give tomatoes with better firmness and can comparatively preserve qualities like color, texture, flavor, and nutritional value [48].

According to Klunklin and Savage [49], high-temperature tolerant local tomato lines that were chosen in a stress affected area had higher levels of lycopene than popular commercial hybrid types. Another study [50] found that tomatoes with higher carotenoid and lycopene content received in the high-temperature application than compared to control. Furthermore, under both control and stress circumstances, sensitive genotypes accumulate less carotenoid and lycopene content than tolerant genotypes [51,52]. Similarly, lycopene concentration and total carotenoids are highly influenced by temperature [53]. Compared to the fruit's physical growth stage, the temperature during the ripening period affects the biosynthesis of lycopene. High temperatures have been shown to cause lycopene degradation, decrease and block biosynthesis [54,55,56]. According to Shi and Maguer [57], lycopene production was suppressed by relatively high temperatures (38°C), whereas low temperatures inhibited the ripening of fruit as well as the formation of lycopene. In this investigation, general drops in tomato lycopene levels were discovered when the temperature was high. Our studies also emphasized on the reduction in the quality related traits like lycopene content, flavanol content and total sugar content in both the categories of tomato genotypes i.e. tolerant and susceptible ones. But the rate of decrease in these attributes were significantly lower in tolerant genotypes when compared to the susceptible ones. It was also noted that the ascorbic acid was increasing when the plants are grown under HS conditions.

The presence of flavonoids and phenolics in tomato fruits can help preserve vitamin C levels because phenolic substances are known to have a protective effect on ascorbic acid content [58,59]. According to Akhoundnejad [60], tomato genotypes' vitamin C content changed in response to high temperatures. Some genotypes showed an increase in vitamin C content, while other genotypes showed a drop. According to Hernández et al. [61], applying temperature stress during the flowering and fruit set stages increased the vitamin C content. They also suggested that there might be a connection

between the adaptation of plant metabolism to high temperatures and the increase in vitamin C. Another investigation on tomato genotypes under high temperature stress found that all tolerant genotypes had increased vitamin C content, whereas susceptible genotypes did not significantly differ in vitamin C content under stress conditions from the control [62].

Stress from high temperatures causes harm to plants due to ROS. Plant tissues have antioxidant enzymes that scavenge ROS, such as catalase, glutathione reductase, superoxide dismutase, and ascorbate peroxidase, as well as nonenzymatic antioxidants such tocopherols, phenolic compounds, and glutathione [63]. ROS detoxification biochemical pathways must be altered in order to achieve thermotolerance, which is why heat stress causes the accumulation of antioxidant molecules such as carotenoids, ascorbic acid (AsA), and polyphenols [64,65]. Additionally, carotenoids can help membranes respond to changes in temperature by enhancing their fluidity and permeability [66,67] In fact, these compounds have the ability to preserve photosynthetic membranes and are crucial for photoprotection, light harvesting, and structural stability.

Phenolics are important secondary metabolites that protect the body from DNA damage, lipid peroxidation, and ROS [68,69]. This study demonstrated that tomato fruit exposed to high temperatures had higher levels of phenolics and displayed antioxidant qualities. In addition to serving as a stress-reduction mechanism for tomato plants, this is a valuable source of antioxidants for humans who eat the fruits of tomato genotypes that can withstand high temperatures [70,71]. Our study showed that the yield parameters were significantly reduced in terms of number of fruits, yield per plant and fruit set percentage and an increase in the intensity of fruit and flower drop ultimately led to reduced fruit yield and quality.

5. CONCLUSION

From this study it can be understood that many of the quality parameters like lycopene content, total sugars, flavanol content was found decreasing in both tolerant and susceptible genotypes but the extend of this reduction was considerate in tolerant ones. In case of ascorbic acid content and firmness of fruit at the time of ripening was increased under HS conditions. Yield related qualities like number of fruits, yield per plant, and root-shoot ratio was found decreasing whereas root dry weight, total dry weight and intensity of fruit drop and flower drop was increased under HS.

With the occurrence of heat waves due to climate change becoming more frequent, this can have an adverse effect on crop yield and quality. Future research must comprehensively investigate nutrient-uptake proteins using molecular analysis, with a specific emphasis on understanding their regulation mechanisms under heat stress conditions. This research should aim to elucidate the impact of such regulation on nutrient concentration and crop quality.

Within this framework, investigating natural variation and identifying genotypes and landraces with high temperature yield performance may aid in comprehending the mechanisms behind high temperature tolerance and offer valuable agronomic traits and genetic diversity for breeding purposes. Consequently, creating new cultivars that can withstand high temperatures is a crucial financial strategy for preparing for impending climate change. Similar to this, there is significant interest in raising the antioxidant content of crops in order to enhance food quality and create high-stress-tolerant varieties. If we are going to develop crops with enhanced tolerance to abiotic stress and higher nutritive value, deeper knowledge on the processes involved in tolerance are necessary. In this respect, the “omics” technologies—genomics, transcriptomics, proteomics metabolomics and phenomics—have proven pivotal for uncovering the key genes, proteins, and metabolic pathways underlying numerous traits of critical agronomic importance.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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