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PHYSIOLOGICAL AND BIOCHEMICAL TRAITS CONTRIBUTING FOR HIGH TEMPERATURE TOLERANCE IN TOMATO (*Solanum lycopersicum* L.)

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ABSTRACT

A study was undertaken to evaluate the physiological and biochemical parameters and to quantify yield of twenty-two contrasting tomato genotypes when exposed to high temperature stress. Experiment was conducted in the Department of Plant Physiology, College of Agriculture, Vellayani during two growing seasons i.e., September to December, 2019 and March to June, 2020. The experiment was laid out in completely randomized design with two treatment levels i.e. control and high temperature stress (36+/-2^{o}C) with three replications each under first season and 38+/-2^{o}C during the second season. The high temperature stress was induced from flower initiation to maturity stage by keeping the pots in a temperature controlled green house facility for 45 days. The presence of stigma exertion, reduction in chlorophyll content and photosynthetic rate, reduced starch content and soluble sugar content, reduced chlorophyll fluorescence, low leaf membrane thermostabilty (LMT) were the major limitations for reproductive success and good yield. The correlation and regression analysis showed that yield under control conditions had strong positive correlation between LMT, pollen viability, photosynthetic rate, chlorophyll fluorescence, starch, soluble sugar and chlorophyll content. A negative correlation was observed between yield and stomatal conductance and transpiration rate. Under high temperature stress condition, all the parameters showed a positive correlation with yield. Based on the performances of various tomato genotypes under control and heat stress conditions, we were able to identify traits that could be manipulated to improve the high temperature tolerance in tomato.

Keywords: Correlation, High temperature, Physiological traits, Tomato, Yield

Tomato (*Solanum lycopersicum* L.) is an important solanaceous vegetable crop which thrives well under tropical and subtropical regions. It is a warm season crop and it requires temperature from 20 to 30^{o}C. After potato and onion, throughout the world tomato is the third mostly produced and consumed vegetable (National Horticultural Board, 2020). Even though tomato can be produced in most of the regions, it confronts many abiotic stress factors especially high temperature nowadays as it directly affects fruit set (Marine *et al.,* 2017).

Intergovernmental Panel on Climate Change (IPCC) predicted an increase of 1-3^{o}C during the twenty first century and during 2090 to 2099 it will be at a range of 1.4 to 6.4^{o}C (IPCC, 2012). Crops require optimum climatic conditions for attaining genetic yield potential so the resulted increase in temperature due to climate change drastically affect the overall growth and yield of crops (Laxman *et al.,* 2013; Beena *et al.,* 2018). The optimum temperature is between 25^{0}C and 30^{o}C during day time and 20^{0} C during night for tomato (Camejo *et al.,* 2005). Temperature above 34^{o}C is considered to be thermal stress according to Ahmed *et al.* (2013). Heat stress adversely affects the vegetative and reproductive process in tomato (Amrutha and Beena, 2020). In tomato temperature above 26 ˚C and 20 ºC during day and night respectively apparently affect the fruit setting and temperature above 38 ˚C and 27 ˚C during day and night respectively often completely arrest it (Amrutha *et al.,* 2021). Under heat stress, the basic physiological processes, such as photosynthesis, assimilate partitioning, growth and development are affected significantly (Chandola, 2016). Flowering phase is most sensitive to extremes of weather. A temperature above 38 ºC for 3-4 hours can cause detrimental effect on crop growth and development of tomato (Archana *et al.,* 2020). Under the prevailing weather conditions of Kerala, the temperature in the summer months can reach up to 38 ºC or more. With this background, the aim of this study was to evaluate the performance of different genotypes of tomato under high temperature condition, to identify the genotype with desirable traits well adapted to be cultivated under high temperature conditions and to identify molecular markers which differentiate tolerant genotypes from susceptible genotypes.

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MATERIALS AND METHODS

This experiment was laid out as a pot culture study in the Department of Plant Physiology, College of Agriculture, Vellayani, Kerala Agricultural University during the year 2019-2020. The genotypes selected for this study are shown in Table 1. Seeds were sown in portrays filled with potting mixture (coir pith compost and vermicompost @ 2:1 ratio) and labelling was done appropriately. Irrigation was provided regularly. Thirty days after sowing, seedlings were transplanted to pots with potting mixture made from soil, sand and cow dung on equal volume by volume basis. Five replications were maintained for each genotype as control and treatment until harvesting stage. The experiment was laid out in completely randomized design with two treatment levels i.e. control and treatment with three replications each. Five plants per replication were maintained. During flower initiation stage one set of all tomato genotypes keeping three replicates per genotype were transferred to stress condition. The experiment was conducted for two growing seasons, the rabi season -September to December (2019) and summer crop – March to June (2020) to study the effect of high temperature on physiological, biochemical, yield parameters in tomato under both seasons and to classify the genotypes under study into different categories like tolerant, moderately tolerant and susceptible genotypes under elevated temperatures. For high temperature stress, temperature was maintained at (36+/-2^{o}C) and (38+/-2^{o}C) for first season and second season respectively. The daily temperatures including maximum and minimum temperatures were recorded under control as well as heat stress conditions using digital thermo-hygrometer throughout the experiment. Physiological and biochemical parameters were taken 25 days after induction of temperature stress. . Physiological parameters and yield traits were taken as per standard procedures using fully expanded leaves ; Chlorophyll content (Hiscox and Israelstam, 1979); Cell membrane stability index (Sullivan, 1972); Pollen viability (Baker and Baker, 1979); Carbohydrate content (Dubois *et al.,* 2002); Starch content (Hodge *et al*., 1962) were also recorded.

Photosynthetic and transpiration rate was measured using portable photosynthetic system (CIRAS-3 SW, PP System International, MA, USA) during day time between 9.00- 10.30 am from the third leaves and were expressed in µmole CO_2 m^{-2} s^{-1}. The presence of stigma exertion were also noticed.

Stomatal conductance (gs, mmol m-2 s-1) measured using an IRGA takes considerable time (generally c. 5 to 10 min per leaf), gs was determined on both leaf surfaces and added to calculate total conductance using infra-red gas analyser (IRGA, Li-Cor Inc., Lincoln, NE, USA). Chlorophyll fluorescence and stomatal conductance were assessed on the top-most mature leaf of each plant.

Chlorophyll fluorescence, defined as the ratio of variable to maximal fluorescence in both dark-adapted (Fv/Fm) and light adapted leaves (Fv'/Fm'), was measured using a Licor 6400XT infra-red gas analyser (IRGA, Li-Cor Inc., Lincoln, NE, USA) fitted with a fluorescence chamber. The leaves were covered with black cloth or aluminium foil about 3 hours before the observation taken to provide the dark adaption. The chlorophyll fluorescence was taken 3 hours after covering by clamping the leaf in the space provided in

Table 1. List of twenty-two tomato genotypes used for the study.

Sl. No.	Genotype	Collected from	Sl. No.	Genotypes	Collected from
1	Nandi	UAS & AVRDC	12	IIHR-26372	IIHR collections
2	IC-45	IIHR collections	13	Palam Pride	HPAU
3	Pusa Rohini	IARI	14	Arka Abha	IIHR
4	Pusa Ruby	IARI	15	Arka Alok	IIHR
5	IIHR-2200	IIHR collections	16	Manulakshmi	KAU
6	Anagha	KAU	17	Sakthi	KAU
7	Akshaya	KAU	18	Manuprabha	KAU
8	Vellayani Vijay	KAU	19	Arka Samrat	IIHR
9	Arka Vikas	IIHR	20	Arka Sourabh	IIHR
10	Kashi Vishesh	ICAR-IIVR	21	PKM-1	TNAU
11	Vaibhav	UAS & AVRDC	22	Arka Rakshak	IIHR

UAS & AVRDC - University of Agricultural Sciences & Asian Vegetable Research and Development Center.
IIHR - ICAR-Indian Institute of Horticultural Research, Bangalore.
IARI – Indian Agricultural Research Institute, New Delhi.
KAU – Kerala Agricultural University, Thrissur.
ICAR-IIVR – ICAR- Indian Institute of Vegetable Research, UP.
HPAU – Himachal Pradesh Agricultural University, Solan.
TNAU- Tamil Nadu Agricultural University, Coimbatore.

photosynthetic system.

Statistical analysis

The statistical analysis and the overall effects of treatment and variety and their interaction were analyzed by two-way ANOVA were done using OPSTAT software (Two factorial CRD) for the two growing seasons. Correlation and regression analysis were carried out for the parameters to study the relationship of the observed parameters and the yield obtained from plants under control as well as high temperature stressed plants grown under the different growing seasons.

RESULTS AND DISCUSSION

The optimum temperature of 20-24°C for normal plant growth and fruit set for tomato during daytime and 15-20°C for night time and minor temperature fluctuations can cause adverse impact on various tomato production (Driedonks *et al.,* 2016). When the environmental temperature is greater than 35°C, seed germination, vegetative growth, flowering and fruit setting get severely affected. The current studies would help to understand the morpho-physiological plasticity under high temperature stress and may identify the traits linked to high temperature stress tolerance for future breeding programmes.

There was variation among the genotypes exhibiting stigma exertion under high temperature. The exerted style, stigma that elongated than the anther cone during reproductive stage reduces self-pollination efficiency. All genotypes under heat stress conditions showed stigma exertion which resulted in flower burning followed by flower drop resulting in reduced fruit yield. Arka Sourabh showed the highest stigma exertion length (Fig. 1). Excessive elongation of the styles in heat sensitive genotypes which perform poorly under elevated heat reduced pollen capacity to reach the stigma and reduced self fertilization and fruit setting rate. In tomato, reproductive stage is the most severely affected stage due to heat stress and reduced yield (Xu *et al.,* 2017). Delayed flowering and fruit maturity was observed in all genotypes under temperature stress condition which may be due to high humidity in the polyhouse condition. But in rice, Sailaja *et al.* (2015) reported that there is decrease in the number of days to 50% flowering and maturity when plants were grown under higher temperatures of 38/28^{o}C. Those genotypes having no stigma exertion at high temperatures are stable and produces good yield (Saeed *et al.,* 2007).

Membrane stability index is a measure of heat tolerance in plants. Under heat stress condition all tomato genotypes showed significant reduction in MSI showing the possibility of increased cell leakage. Among plants under control condition, Nandi (87.63%) showed the highest MSI and minimum was recorded in Arka Sourabh (7.62%) whereas under heat stress Nandi (51.8%) and Arka Rakshak (25.13%) showed maximum and minimum MSI respectively for heat stress conditions, during the *rabi* season (Figure 2). The percentage reduction in MSI was highest in Pusa Ruby (52%) and lowest in IIHR-2200 (11%). Oxidative stress causes peroxidation of membrane lipids, proteins, and nucleic acids. Due to reduced membrane stability, electrolyte leakage increases, which intensifies the membrane injuries (Alsamir *et al.,* 2017; Vijayakumar *et al.,* 2021). During the next growing season, similar results were obtained under control conditions with highest MSI for Nandi and lowest in Arka Sourabh which was 80.60% and 10.30% respectively. Under stress conditions, Nandi and Arka Sourabh showed MSI of 48.64% and 20.40% respectively. Saeed *et al.* (2014) carried out an experiment in which varieties with greater tolerance to heat stress showed higher membrane thermostability. This can be related with our studies too, as genotypes having tolerance capacity under heat stress environments showed a higher MSI values then those susceptible genotypes which showed

Fig. 1. Stigma exertion in Arka Sourabh b, Arka Sourabh flower under control condition (left) and under heat stress condition (right) showing exerted stigma.

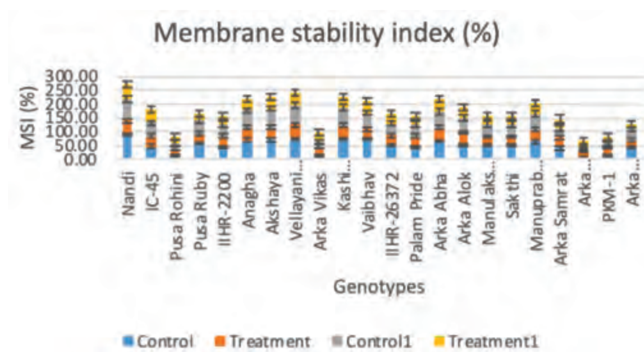


Fig. 2. Membrane stability index of tomato genotypes under control and high temperature stress conditions for different growing season expressed in percentage.

a significant reduction in MSI values when under stress conditions.

A decrease in pollen production, release, viability, germination, fruit set of tomato at temperatures above optimum temperature has been studied by various scientists (Sato *et al.,* 2001; Pressman *et al.,* 2002). Pollen viability was maximum for Anagha (97.45%) and minimum for Arka Vikas (88.91%) under control conditions but for high temperature condition pollen viability reduced significantly for all genotypes with minimum reduction in viability value for Nandi with 87.38% and maximum in Arka Vikas (36.31%) during Rabi (Table 2). Pollen viability during second growing season was maximum for Nandi (88.75%) and minimum for Arka Rakshak (63.24%).

Significant variation were examined for total chlorophyll content among the genotypes and between the treatments. Total chlorophyll content was highest for Arka Alok (2.3 mg g^{-1} fresh weight) and lowest was recorded by Arka Vikas (1.28 mg g^{-1} fresh weight) under control condition and it was highest and lowest in case of Arka Alok (0.71 mg g^{-1} fresh weight) and Arka Samrat (0.36 mg g^{-1} fresh weight) (Fig. 3) respectively under heat stress. In case of stressed second season condition, total chlorophyll content was maximum for Akshaya (1.29 mg g^{-1} fresh weight) and minimum for Arka Vikas (0.58 mg g^{-1} fresh weight) whereas, Kashi Vishesh (20.05 mg g^{-1} fresh weight) and IIHR-26372 (14.90 mg g^{-1} fresh weight) showed highest and lowest values respectively under control conditions. The decrease in chlorophyll content under stress condition may be due to stress-induced disruption in biosynthetic pathways or in pigment degradation, loss of the

Table 2. Pollen viability of tomato genotypes under control and high temperature stress conditions expressed in percentage.

	Sept-Dec			Mar-Jun		
Genotype	**Control**	**Treatment**	**Mean**	**Control**	**Treatment**	**Mean**
Nandi	95.01	87.38	91.19	92.20	85.30	88.75
IC-45	95.33	79.82	87.57	93.00	77.50	85.25
Pusa Rohini	90.08	44.33	67.2	87.12	42.22	64.67
Pusa Ruby	94.82	47.77	71.3	86.30	46.10	66.20
IIHR-2200	94.17	50.33	72.25	92.37	48.28	70.33
Anagha	97.45	50.81	74.13	94.37	49.39	71.88
Akshaya	95.81	54.21	75.01	93.00	52.45	72.73
Vellayani Vijay	96.25	63.33	79.79	85.59	60.62	73.10
Arka Vikas	88.91	36.31	62.61	81.43	34.03	57.73
Kashi Vishesh	96.2	52.34	74.27	87.93	49.67	68.80
Vaibhav	95.05	64.56	79.8	85.23	55.77	70.50
IIHR-26372	94.94	58.56	76.75	71.73	56.17	63.95
Palam Pride	95.88	48.48	72.18	87.00	44.57	65.78
Arka Abha	94	44.72	69.36	91.10	42.87	66.98
Arka Alok	95.03	53.76	74.39	91.17	48.14	69.66
Manulakshmi	95.43	46.04	70.74	92.08	43.04	67.56
Sakthi	92.29	42.63	67.46	90.32	40.65	65.49
Manuprabha	97.19	49.39	73.29	93.02	46.02	69.52
Arka Samrat	95.66	42.08	68.87	93.58	38.43	66.01
Arka Sourabh	91.69	39.72	65.7	89.77	38.05	63.91
PKM-1	92.09	49.07	70.58	90.07	45.72	67.89
Arka Rakshak	89.92	45.49	67.71	87.13	39.35	63.24
Mean	94.24	52.32		88.89	49.29	
Factors	SE(m)	C.D. (0.5%)		SE(m)	C.D. (0.5%)	
Varieties	1.46	4.12		1.31	3.69	
Treatments	0.44	1.24		0.40	1.11	
Factor (V X T)	2.07	5.83		1.85	5.22	

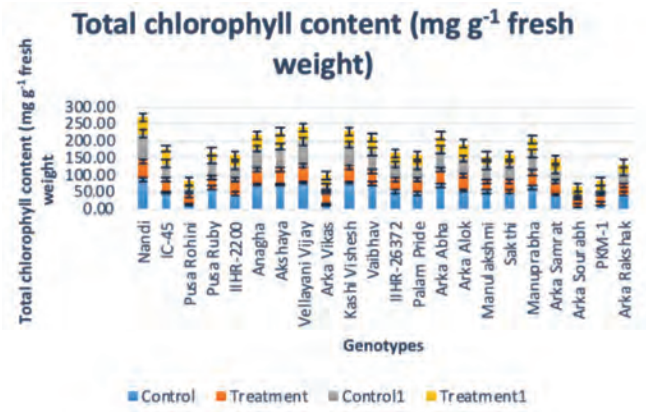


Fig. 3. Total chlorophyll content of tomato genotypes under control and high temperature stress conditions for different growing season expressed in mg g^{-1} fresh weight.

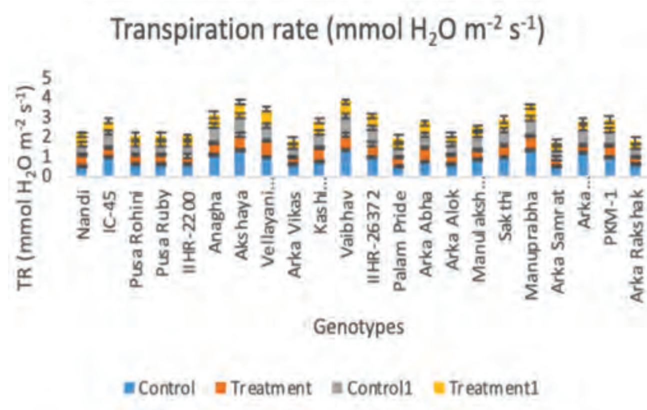


Fig. 4. Transpiration rate (E) of tomato genotypes at flowering stage under control and high temperature stress conditions for different growing season expressed in mmol H_2O m^{-2} s^{-1}.

chloroplast membrane, and increased lipid peroxidation thus resulting in production of reactive oxygen species (ROS) (Reda and Mandoura, 2011). Our study also supported this view, that reduction in the photosynthetic rate may be associated to the reduced chlorophyll content. Higher values of photosynthetic rates can be attributed to higher yields under stress conditions and are correlated positively.

Photosynthetic rate reduced significantly in all the genotypes under heat stress condition compared to control (Table 3). Under heat stress condition, Arka Alok (19.07 µ CO_2 moles m^{-2} s^{-1}), Arka Abha (14.20 µ CO_2 moles m^{-2} s^{-1}) highest and lowest photosynthetic rate in heat stress conditions and Vellayani Vijay (23.03 µ CO_2 moles m^{-2} s^{-1}) and Manuprabha (16.93 µ CO_2 moles m^{-2} s^{-1}) showed highest and lowest photosynthetic rate in heat stress and control condition respectively during first crop. The mean photosynthetic rate of tomato genotypes was 19.76 µ CO_2 moles m^{-2} s^{-1} and 16.13 µ CO_2 moles m^{-2} s^{-1} under control and heat stress conditions respectively. During the second season, photosynthetic rate showed drastic reduction in their values. Highest photosynthetic rate was reported in Kashi Vishesh (20.05 µ CO_2 moles m^{-2} s^{-1} and 15.59 µ CO_2 moles m^{-2} s^{-1}) under control as well as high temperature stress conditions. In contrast, the lowest values was reported for IIHR-26372 (14.90 µ CO_2 moles m^{-2} s^{-1}) under control conditions and Arka Abha (11.27 µ CO_2 moles m^{-2} s^{-1}) under heat stress condition (Table 3). Tomato cultivars under two temperature regimes (37/27 °C or 37/22 °C day/night) showed that the tolerant cultivars showed better photosynthetic rate under heat stress conditions at different growth stages in comparison to the heat sensitive ones (Abdelmageed and Gruda, 2009). Kashi Vishesh under control as well as high temperature stress conditions had the highest photosynthetic rate and Arka Vikas under heat stress condition showed minimum photosynthetic rate suggesting the performance of tomato genotypes based on their heat tolerance capacity.

There was significant variation for transpiration rate among the genotypes and between treatments (Fig. 4). Highest and lowest transpiration rate were recorded for Vaibhav (1.36 mmol H_2O m^{-2} $s^{-1)}$ and Palm Pride (0.49 mmol H_2O m^{-2} sec^{-1}) for control plants whereas, Vellayani Vijay and Arka Rakshak showed highest and lowest transpiration rates under high temperature stress which was 0.83 mmol H_2O m^{-2} $s^{-1}$and 0.35 mmol H_2O m^{-2} s^{-1} respectively in the first growing season (Fig. 6). The average transpiration rate of tomato genotypes were 0.55 and 0.85 mmol H_2O m^{-2} s^{-1} for heat stress and control condition respectively. Vaibhav (1.02 mmol H_2O m^{-2} s^{-1}) and Arka Rakshak (0.32 mmol H_2O m^{-2} $s^{-1)}$ recorded the highest and lowest values under control and heat stress conditions respectively for control. The reduction in transpiration rate was minimum for the tolerant genotypes like Vaibhav and maximum for the sensitive ones like Arka Rakshak (Shaheen *et al.,* 2015).

The results revealed that stomatal conductance decreased significantly in almost all the genotypes under stress condition as compared to control. The highest and lowest values were observed for Arka Rakshak (78 mmol H_2O m^{-2} s^{-1}) and Arka Sourabh (43.33 mmol H_2O m^{-2} s^{-1}) for under normal conditions whereas, it was maximum for Nandi and Vellayani Vijay (63.33 mmol H_2O m^{-2} s^{-1}) and minimum for Arka Sourabh (32 mmol H_2O m^{-2} s^{-1}) under heat stress conditions. The mean stomatal conductance of tomato genotypes was 62.86 mmol H_2O m^{-2} s^{-1} and 46.30 mmol H_2O m^{-2} s^{-1} under control and heat stress conditions, respectively. In case of second crop, the highest value was observed for Arka Vikas and lowest for Arka Sourabh which was

Table 3. Photosynthetic rate of tomato genotypes under control and high temperature stress conditions for different growing season expressed in μ CO_2 moles m^{-2} s^{-1}.

	Sept-Dec			Mar-Jun		
Genotype	Control	Treatment	Mean	Control	Treatment	Mean
Nandi	20.31	17.03	18.67	18.17	14.59	16.38
IC-45	18.69	15.52	17.11	15.79	12.74	14.27
Pusa Rohini	18.10	14.85	16.48	15.23	11.95	13.59
Pusa Ruby	19.20	16.39	17.79	15.26	13.00	14.13
IIHR-2200	20.18	18.13	19.16	16.08	14.18	15.13
Anagha	21.12	17.75	19.43	15.85	15.11	15.48
Akshaya	21.83	17.70	19.77	18.50	15.48	16.99
Vellayani Vijay	23.03	17.97	20.50	18.18	15.22	16.70
Arka Vikas	18.79	14.10	16.45	15.76	12.86	14.31
Kashi Vishesh	21.76	18.63	20.20	20.05	15.59	17.82
Vaibhav	20.95	15.63	18.29	19.49	13.47	16.48
IIHR-26372	18.33	14.37	16.35	14.90	12.19	13.55
Palam Pride	21.05	14.70	17.87	18.64	11.68	15.16
Arka Abha	18.23	14.20	16.22	15.74	11.27	13.51
Arka Alok	21.75	19.22	20.49	16.25	14.50	15.37
Manulakshmi	19.23	17.33	18.28	17.06	14.47	15.76
Sakthi	17.70	15.63	16.67	16.22	13.49	14.85
Manuprabha	16.93	14.43	15.68	15.99	12.33	14.16
Arka Samrat	20.81	17.00	18.91	17.77	12.90	15.34
Arka Sourabh	18.29	14.30	16.30	15.72	12.14	13.93
PKM-1	18.73	15.47	17.10	16.22	14.10	15.16
Arka Rakshak	19.75	14.59	17.17	18.48	13.02	15.75
Mean	19.76	16.13		16.88	13.47	
Factors	SE(m)	C.D. (0.5%)		SE(m)	C.D. (0.5%)	
Varieties	0.35	1.00		0.39	1.11	
Treatments	0.11	0.30		0.12	0.33	
Factor (V X T)	0.50	1.41		0.56	1.57	

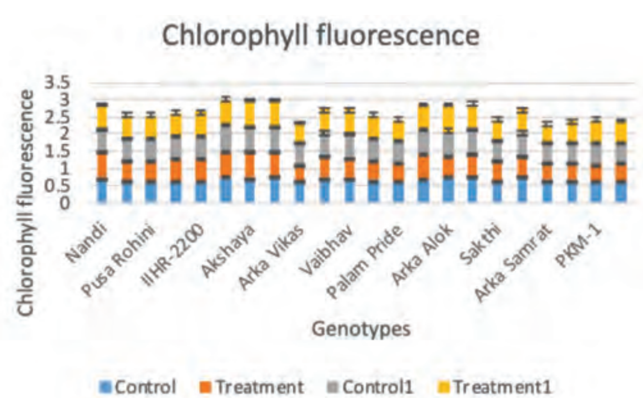


Fig. 5. Chlorophyll fluorescence of tomato genotypes under control and high temperature stress conditions for different growing season expressed in mmol H_2O m^{-2} s^{-1}.

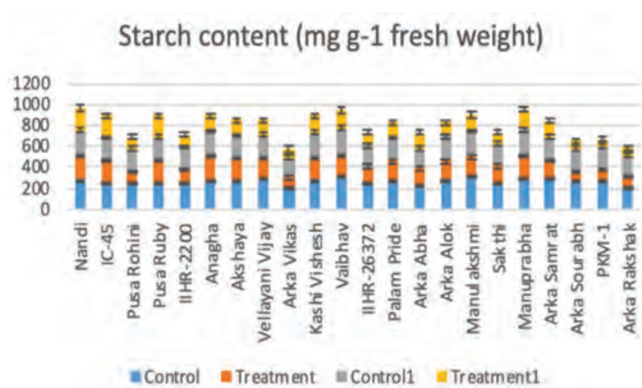


Fig. 6. Starch content in leaves of tomato genotypes under control and high temperature stress conditions for different growing season expressed in mg g^{-1} fresh weight.

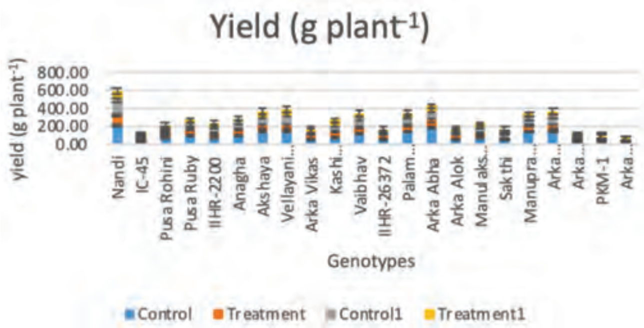


Fig. 7. Yield of tomato genotypes under control and high temperature stress conditions for different growing season expressed in mmol H_2O m^{-2} s^{-1}.

84.33 mmol H_2O m^{-2} s^{-1} and 39.67 mmol H_2O m^{-2} s^{-1} respectively for control conditions whereas it is highest and lowest for Nandi (58.67 mmol H_2O m^{-2} s^{-1}) and Arka Sourabh (30 mmol H_2O m^{-2} s^{-1}) for heat stress conditions. A decrease in the stomatal conductance was observed among all genotypes (Camejo *et al.,* 2005b), and maximum reduction was observed for sensitive genotypes like Arka Sourabh, Arka Rakshak and minimum reduction for tolerant genotypes like Nandi, Kashi Vishesh, Vellayani Vijay. The significant reduction in stomatal conductance was highest in case of sensitive genotypes under stress condition than compared to control conditions which supported our findings .

Among the genotypes, it was observed that in previous reports in tomato, Fv/Fm under control condition was higher than Fv/Fm under stress condition (Zhou *et al.,* 2015). Nandi (0.75) and Anagha (0.75) recorded the maximum chlorophyll fluorescence, while Arka Vikas and Arka Sourabh (0.46) exhibited the minimum chlorophyll fluorescence for stressed ones. For ambient condition, Anagha, Vellayani Vijay, Arka Alok, Manulakshmi and Manuprabha (0.74) showed maximum, while in Palam Pride (0.62) minimum value was accorded. The average chlorophyll fluorescence of the tomato genotypes at flowering stage was 0.6 and 0.68 under heat stress and control conditions respectively. Anagha, Akshaya, Vellayani Vijay and Arka Alok (0.75) showed maximum value and Arka Samrat (0.56) showed minimum value for control but Anagha, Akshaya, Vellayani Vijay (0.76) and Arka Vikas (0.60) showed the highest and lowest values for stress (Fig. 5). Under abiotic stress condition especially heat stress, a decline in chlorophyll fluorescence is observed (Sharma *et al.,* 2014) similar to the present results. This decline may be due to non-photochemical quenching due to the photo-inactivation of PS II, which denote decrease in Fm and increase in Fo.

Among the genotypes, starch content was found highest in Vaibhav (312.97 mg g^{-1} fresh weight) and minimum in Arka Rakshak (214.06 mg g^{-1} fresh weight) under control conditions whereas, Anagha (235.67 mg g^{-1} fresh weight) and Arka Sourabh (84.37 mg g^{-1} fresh weight) recorded highest and lowest content under stressed conditions. For the control plants of second

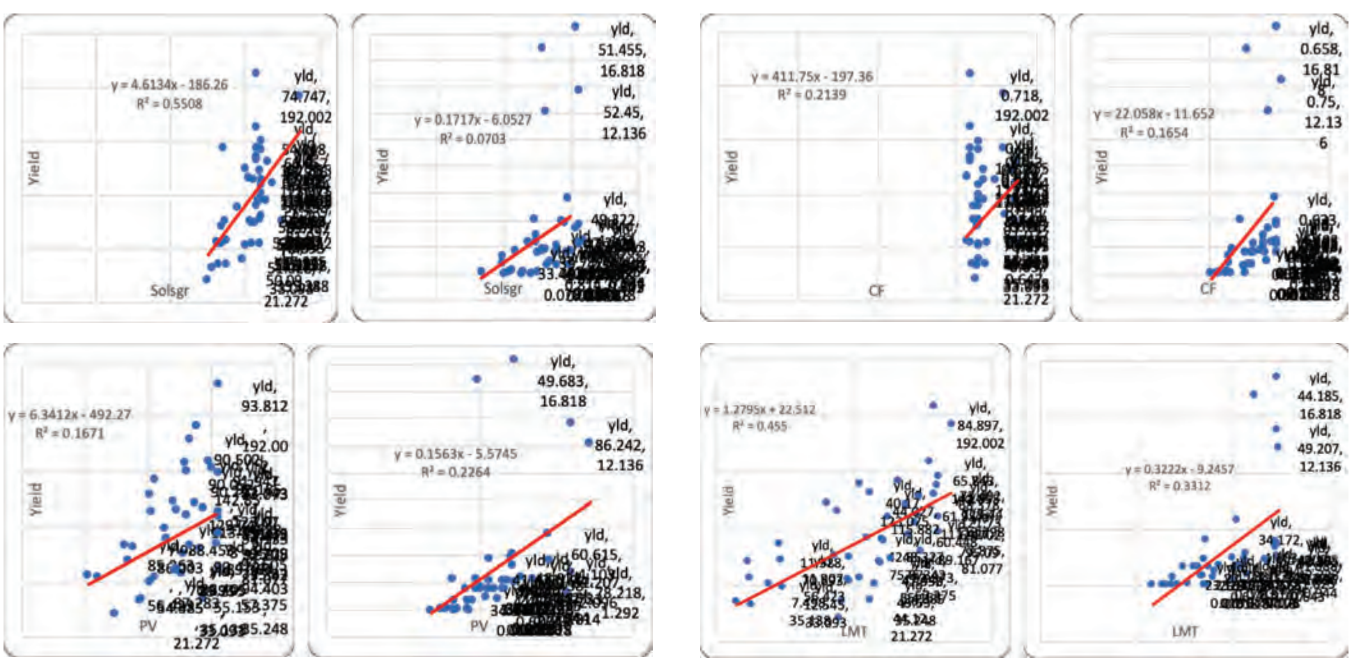


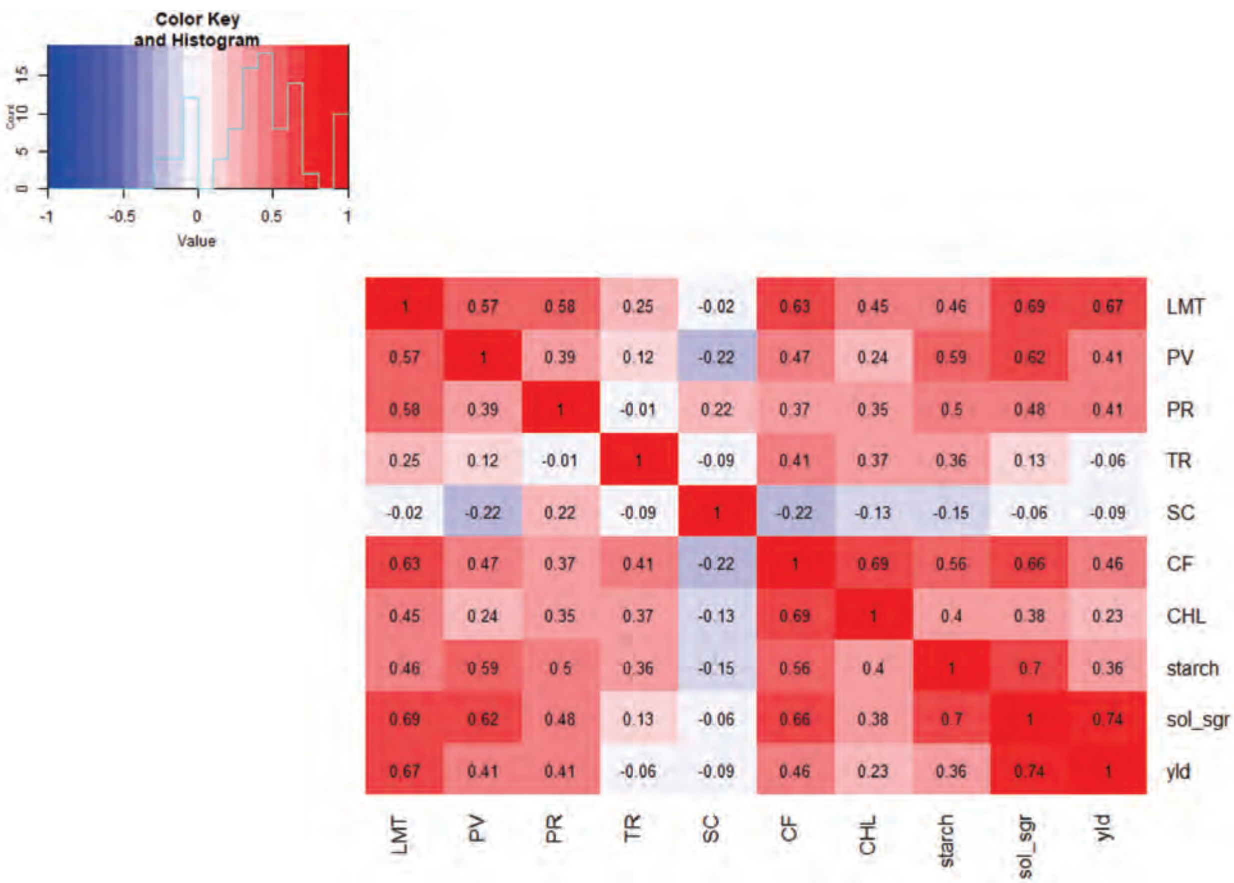
Fig. 8. Regression relationship of different parameters under both control (left) and high temperature conditions (right) which are significant with fruit yield. a) Soluble sugar b) Chlorophyll fluorescence c) Pollen viability d) Leaf membrane thermostability.

Table 4. Soluble sugar content in leaves of tomato genotypes under control and high temperature stress conditions expressed in mg g^{-1} fresh weight.

Genotype	Sept-Dec			Mar-Jun		
	Control	Treatment	Mean	Control	Treatment	Mean
Nandi	77.73	53.65	65.69	72.30	51.87	62.08
IC-45	57.52	41.54	49.53	50.88	40.24	45.56
Pusa Rohini	56.03	41.35	48.69	52.09	38.40	45.25
Pusa Ruby	60.65	49.38	55.02	52.61	47.17	49.89
IIHR-2200	57.23	55.53	56.38	54.61	52.04	53.32
Anagha	66.43	49.74	58.09	61.42	55.38	58.40
Akshaya	65.88	56.82	61.35	60.74	53.39	57.07
Vellayani Vijay	67.79	59.60	63.70	61.87	57.40	59.64
Arka Vikas	53.41	46.41	49.91	49.24	43.36	46.30
Kashi Vishesh	65.99	53.30	59.65	63.63	60.77	62.20
Vaibhav	63.67	51.06	57.36	61.49	47.79	54.64
IIHR-26372	54.58	42.33	48.46	52.87	38.14	45.51
Palam Pride	61.80	42.80	52.30	59.86	41.93	50.90
Arka Abha	55.91	50.07	52.99	54.31	43.24	48.78
Arka Alok	57.40	53.46	55.43	55.04	47.39	51.22
Manulakshmi	72.03	56.81	64.42	56.74	53.12	54.93
Sakthi	56.96	45.80	51.38	53.21	43.47	48.34
Manuprabha	71.83	52.91	62.37	66.68	47.38	57.03
Arka Samrat	62.56	43.98	53.27	55.24	39.09	47.17
Arka Sourabh	54.94	46.30	50.62	50.55	47.49	49.02
PKM-1	53.83	45.61	49.72	52.21	40.87	46.54
Arka Rakshak	51.92	35.73	43.83	49.10	31.51	40.31
Mean	61.19	48.83		56.67	46.43	
Factors	SE(m)	C.D. (0.5%)		SE(m)	C.D. (0.5%)	
Varieties	0.98	2.75		0.68	1.92	
Treatments	0.29	0.83		0.21	0.58	
Factor (V X T)	1.38	3.89		0.96	2.71	

season, Vaibhav (262 mg g^{-1} fresh weight) and Arka Vikas (187.66 mg g^{-1} fresh weight) recorded the highest and lowest values whereas, for heat stress conditions, Nandi and PKM-1 had 211.29 mg g^{-1} fresh weight and 65.63 mg g^{-1} fresh weight which were highest and lowest values respectively (Fig. 6). Heat stress reduces the accumulation of sucrose in the leaves of both heat tolerant and heat-sensitive tomato genotypes, indicating that carbohydrate assimilation and partitioning to other plant parts are negatively impacted by high temperatures, similar to results in other crops like rice and chilli (Shanmugam *et al.,* 2013; Pravallika *et al.,* 2020).

Soluble sugar content in tomato showed significant genotypic differences were observed for heat stress condition. For this parameter under control, Nandi and Arka Rakshak showed highest and lowest values which is 77.73 mg g^{-1} fresh weight and 51.92 mg g^{-1} fresh weight respectively whereas under stress conditions, Vellayani Vijay and Arka Rakshak recorded 59.6 mg g^{-1} fresh weight and 35.73 mg g^{-1} fresh weight which is highest and lowest (Table 4). For stressed plants of second season, Nandi (72.30 mg g^{-1} fresh weight) and Arka Rakshak (49.10 mg g^{-1} fresh weight) showed the highest and lowest respectively but under heat stress conditions, Kashi Vishesh (60.77 mg g^{-1} fresh weight) and Arka Rakshsk (31.51 mg g^{-1} fresh weight) showed highest and lowest values. For heat stressed plants the concentration of starch and soluble sugar reduce in a greater amounts than that under control conditions (Kumar *et al.,* 2015). The results obtained are in consonance with earlier studies and the carbohydrate



	LMT	PV	PR	TR	SC	CF	CHL	starch	sol_sgr	yld
LMT	1	0.57	0.58	0.25	-0.02	0.63	0.45	0.46	0.69	0.67
PV	0.57	1	0.39	0.12	-0.22	0.47	0.24	0.59	0.62	0.41
PR	0.58	0.39	1	-0.01	0.22	0.37	0.35	0.5	0.48	0.41
TR	0.25	0.12	-0.01	1	-0.09	0.41	0.37	0.36	0.13	-0.06
SC	-0.02	-0.22	0.22	-0.09	1	-0.22	-0.13	-0.15	-0.06	-0.09
CF	0.63	0.47	0.37	0.41	-0.22	1	0.69	0.56	0.66	0.46
CHL	0.45	0.24	0.35	0.37	-0.13	0.69	1	0.4	0.38	0.23
starch	0.46	0.59	0.5	0.36	-0.15	0.56	0.4	1	0.7	0.36
sol_sgr	0.69	0.62	0.48	0.13	-0.06	0.66	0.38	0.7	1	0.74
yld	0.67	0.41	0.41	-0.06	-0.09	0.46	0.23	0.36	0.74	1

Table 5. Correlation matrix (control)

Table 6. Classification of tomato genotypes based on important yield and physiological traits as indicators of heat tolerance into tolerant genotypes, moderately tolerant and susceptible genotypes

Varieties	Pollen viability	Thermostability	Starch	Photosynthetic rate	Stomatal conductance	Chlorophyll fluorescence	Yield
KV, VV, ND, VB	50-70%	60-70%	190-230	17-22	47-68	0.6-0.8	50-60
AK, IIHR2200,MP	45-50%	40-50%	<200	17-19	55-65	0.6-0.8	10-30
SB, RK, RH, PP	44-45%	25-40%	90-110	13-16	30-37	0.4-0.5	0.5-5

deprivation may be responsible for the stress-induced pollen abortion or sterility (Firon *et al.,* 2006).

There was significant difference among genotypes and between genotypes for yield per plant. Nandi (639.36g/plant) and Arka Abha (539.83g/plant) recorded the highest yield under control condition whereas, Arka Rakshak (67.23g/plant) recorded the lowest yield. Under heat stress conditions Kashi Vishesh (79.31g/plant) and Nandi (56.7g/plant) produced the highest yield (Fig. 7). During the second season, reduction in yield was found in great extend for susceptible genotypes than tolerant ones (Amrutha *et al.,* 2021).

Regression analysis

Simple linear regression analysis revealed that there is a significant linear increase in the yield of tomato genotypes with the increasing soluble sugar content which showed similarity with the previous studies (Kumar *et al.,* 2015) (Fig. 8). The linear regression line indicated a linear increase in the yield with the increasing chlorophyll fluorescence reported earlier (Mathur *et al*., 2014). In case of linear regression line for the yield and pollen viability, there is a significant positive relationship (Marine *et al*., 2017). When the LMT increases there is a hike in the yield of tomato which indicated a significant positive linear relation as indicated by Ismail and Hall (1999); Alsamir *et al.* (2017).

Correlation analysis

Correlation coefficient is a statistical measure, which is used to know the degree and indicates relationship between two or more variables. The degree of association also affects an effectiveness of selection process. The data on various traits which were recorded under the ambient and heat stress conditions in tomato genotypes were subjected to correlation analysis.

Under control conditions, strong positive correlation was observed between LMT, pollen viability, photosynthetic rate, chlorophyll fluorescence, starch, soluble sugar and chlorophyll content with the yield of plants. A negative correlation were observed between yield and stomatal conductance and transpiration rate. But for high temperature condition, all the parameters showed a positive correlation with yield.

Control condition

Correlation between different traits and yield under control condition is represented in Table 5. Under control condition, tomato yield was found to be positively correlated with physiological parameters such as membrane stability index (r = 0.67), photosynthetic rate (r = 0.41), chlorophyll fluorescence (r = 0.46), pollen viability (r = 0.41), total chlorophyll content (r = 0.23), starch content (r = 0.36), soluble sugar content (r = 0.74). Significant negative correlation was observed between yield and transpiration rate (r = -0.06) and stomatal conductance (r = -0.09) under control condition**.**

High temperature condition

Correlation study revealed that tomato yield per plant under heat stress condition was positively correlated with membrane stability index (r = 0.28), photosynthetic rate (r = 0.57), chlorophyll fluorescence (r = 0.41), pollen viability (r = 0.48), total chlorophyll content (r = 0.10), starch content (r = 0.48), soluble sugar content (r = 0.27), transpiration rate (r = 0.37) and stomatal conductance (r = 0.52) under heat stress condition**.**

From this study, it can be found that membrane stability index, pollen viability and stomatal conductance are the major factors limiting tomato fruit set under heat stress conditions and should be a target for further studies. With respect to yield and physiological data the varieties sharing similar characteristics can be classified under three categories *viz,* tolerant varieties, moderately tolerant and susceptible varieties (Table 6). Tolerant genotypes (Nandi, Kashi Vishesh, Vellayani Vijay) exhibited similar characteristics like yield (10-30 g^{-1} plant), MSI (60-70 %), PV (50-70%), starch content (190-200 mg g^{-1} fresh weight), A (17-22 µmol CO_2 m^{-2} sec^{-1}), Gs (47-68 mmol H_2O $m^{-2}sec^{-1}$), CF (Fv / Fm) (0.6-0.7). Moderately tolerant varieties (Akshaya, Manuprabha, IIHR-2200, Vaibhav) showed similar characteristics like yield (5-15 g^{-1} plant), MSI (40-50 %), PV (45-50 %), starch content (200 mg g^{-1} fresh weight), A (17-19 µmol CO_2 m^{-2} sec^{-1}), Gs (55-65 mmol H_2O $m^{-2}sec^{-1}$), CF(Fv / Fm) (0.6-0.7) and susceptible varieties (Arka Vikas, Pusa Rohini, Arka Sourabh, Arka Rakshak) showed similar features like yield (0.5-5 g^{-1} plant), MSI (25-40 %), PV (44-45 %), starch content (90-110 mg g^{-1} fresh weight), A (13-16 µmol CO_2 m^{-2} sec^{-1}), Gs (30-37 mmol H_2O $m^{-2}sec^{-1}$) and CF (0.4-0.5). Development of heat tolerant tomato lines is the major objective in tomato breeding particularly in the present scenario of global warming. A line that possesses all the important physio-biochemical traits must be developed to enhance the thermo-tolerance, so that the plant can give moderately higher yield even under high temperatures.

Authors' contribution

Conceptualization and designing of the research work (AV); Execution of field/lab experiments and data collection (AV); Analysis of data and interpretation (AV, BR, SS); Preparation of manuscript (BR,AV).

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