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Response of tomato (*Lycopersicon esculentum* Mill.) genotypes to elevated temperature

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ABSTRACT

Global warming is an important issue threatening agriculture and allied sectors with serious consequences on food production. Tomato being sensitive to temperature would be influenced by elevated temperatures under climate change scenarios. Physiological response of five tomato genotypes, Arka Vikas, Arka Saurabh, Abhinava, RF4A and 2195 to mild elevated temperatures at peak flowering and peak fruiting stages was evaluated in temperature gradient tunnel (TGT) facility. The increase in temperature above the optimal, caused reductions in net photosynthesis rate, transpiration and stomatal conductance with differences in response among the five genotypes. The reductions were large at peak flowering stage compared to peak fruiting stage. The Photochemical efficiency of PSII was also reduced at both peak flowering and fruiting stages due to increase in temperature. At peak fruiting stage, due to increase in temperature, leaf epicuticular wax content increased across the genotypes and higher total soluble sugars, reducing sugars and proline content contributed to increase in leaf osmotic potential. Overall, better performance of germplasm line 2195 and cv. Arka Vikas was observed under elevated temperature.

Key words: Climate change, elevated temperature, tomato, TGT, cholorophyll florescence

The Fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC) estimated that the current global mean surface temperature is about 0.42 to 0.54 °C above the 1961-1990 annual average and multi model averages indicated the temperature increases in the range from 1.1 to 6.4 °C during 2090-2099 relative to 1980 to 1999 (IPCC, 2007). The increase in temperature under climate change situations would considerably influence crop yields and in turn the sustained supply to meet growing demands. Crop plants need optimum growing conditions for attaining genetic yield potential. However, the occurrence of abiotic stresses at critical growth stages seldom allows crops to attain genetic yield potential and global climate change further threatens sustenance of crop yields. Tomato is an important horticultural crop in India; currently it is the second largest produced vegetable. This feat has been achieved with country wide area of 8.65 lakh ha with 168.26 lakh tons production. Optimal mean daily temperatures for tomato are between 21 and 24 °C, depending on developmental stage (Geisenberg and Stewart, 1986). The optimum temperature for net assimilation rate is between 25-30 °C (Khavari-Najad, 1980). Temperatures only a few degrees above optimal can reduce fruit production and seed set in tomato (Peet *et al*., 1997).

Supra optimal temperatures cause a series of complex morphological, physiological, biochemical and molecular changes that adversely affect plant growth and productivity (Wang *et al*., 2003). Photosynthesis can be completely inhibited by high temperature before other symptoms are detected (Berry and Bjorkman, 1980). Some studies on the effect of elevated temperatures on tomato have been conducted with extremely high temperatures. Camejo *et al*. (2005) subjected two tomato genotypes to 45 °C for two hours and observed the reductions in photosynthesis rate and the photochemical efficiency of PSII (Fv/Fm) in the heat susceptible tomato cultivar, Campbell-28. In another study, Heckathorn *et al*. (1998) exposed tomato plants to 43 °C for 6 hours and reported significant reductions in PSII electron transport. On the contrary some studies have been conducted under high and moderately high temperatures. In a study on effect of two temperature regimes, 37/27 °C and 37/22 °C, Abdelmageed and Gruda (2009) reported differences in photosynthesis rate among eight genotypes with reduction at higher temperature regime. Exposing tomato plants to moderately high temperature of 35 °C for eight hours caused decreased photosynthetic activity and changes in carbohydrate metabolism (Zhang *et al*., 2012). Studies on the effect of chronic mild heat stress (32/26 °C) on five tomato cultivars showed that generally, in all the five cultivars, photosynthesis rate was lower in plants kept at 32/26 °C compared to plants kept at 28/22 °C. However, there was no significant relationship between photosynthesis rate and fruit set. All these studies have shown the influence of temperatures slightly above the optimal on photosynthetic

machinery of tomato genotypes. The present study was conducted with an objective to evaluate the physiological response of five tomato genotypes to mild elevated temperature.

MATERIALS AND METHODS

The study was carried out during the months of October 2011 to February 2012 at Indian Institute of Horticulture Research (IIHR), Bangalore, Karnataka, India (12.97°N and 77.56°E). Five tomato (*Lycopersicon esculentum* Mill.) genotypes were selected for the study. Cultivar Arka Vikas was selected as it is adapted to both rainfed and irrigated conditions and grown in all the three seasons. Cultivar Arka Saurabh was selected as it is suitable for *kharif* and *rabi* seasons not for summer season due to susceptibility to Tomato Leaf Curl Virus (TLCV). Commercial hybrid Abhinava which is suitable for summer season was included for comparison. Based on previous performance advanced breeding lines, RF4A which shows tolerant to moisture stress and 2195 with tolerance to high temperature were selected. The seeds were sown in pro-trays with coco peat as the growing medium in the nursery. Twenty five day old seedlings were transplanted to 20 liter capacity plastic containers filled with soil, FYM and sand in the ratio of 2:1:1. Temperature Gradient Tunnel (TGT) with dimensions of 18 m length, 4.5m width and 3 m height covered with polycarbonate sheet was used for the study. One week after transplanting, the containers were shifted to the TGT for imposition of temperature treatments. One set of six plants each for all the five genotypes was placed near the cooling pad and another set with same number of plants was placed towards the fan where the average air temperatures were about 2°C higher. The average weekly temperature and relative humidity (RH) recorded inside the TGT are given in Fig. 1. The gradient inside the TGT was maintained only during the day time as the TGT worked on pad and fan system. Since there was no gradient in the night time minimum temperatures, only one average temperature is given (Fig. 1). Photosynthetic Active Radiation (PAR) available inside the TGT was about 85 per cent. The plants were provided with recommended fertilizer dose and crop protection measures were taken as and when required.

The gas exchange parameters were measured between 9300 h and 1100 h at peak flowering and peak fruiting stages, ie., 34 and 64 days after shifting the plants to TGT for imposition of temperature treatments, using Portable Photosynthesis System, LI-6400 Xt (LiCor. Lincoln, Nebraska, USA). The CO_2 concentration was maintained at 380 µ mol mol $^{-1}$ to avoid CO_2 fluctuations inside TGT and external light of 1200 µmol m^{-2} s^{-1} was supplied by red-blue LED light source. Chlorophyll fluorescence was measured between 1000 h and 1100 h at peak flowering and peak fruiting stages after a dark adaptation period of 30 minutes by Portable Pulse Modulated Fluorimeter (GFS 3000, Heinz Walz GmbH, Germany). The leaf total soluble sugars (Dubois *et al*., 1956), reducing sugars (Somogyi, 1952), epicuticular wax content (Ebercon *et al.,* 1977) and proline content (Bates *et al.,* 1973) were determined at peak fruiting stage.

Statistical analyses were performed using SPSS package (SPSS Inc. version 16.0) for all sets of data and means were compared using Duncan multiple comparison test at P = 0.05.

RESULTS AND DISCUSSION

The gas exchange parameters, net photosynthesis rate (P_N), stomatal conductance (gs) and transpiration rate (E) decreased at peak flowering stage due to increase in air

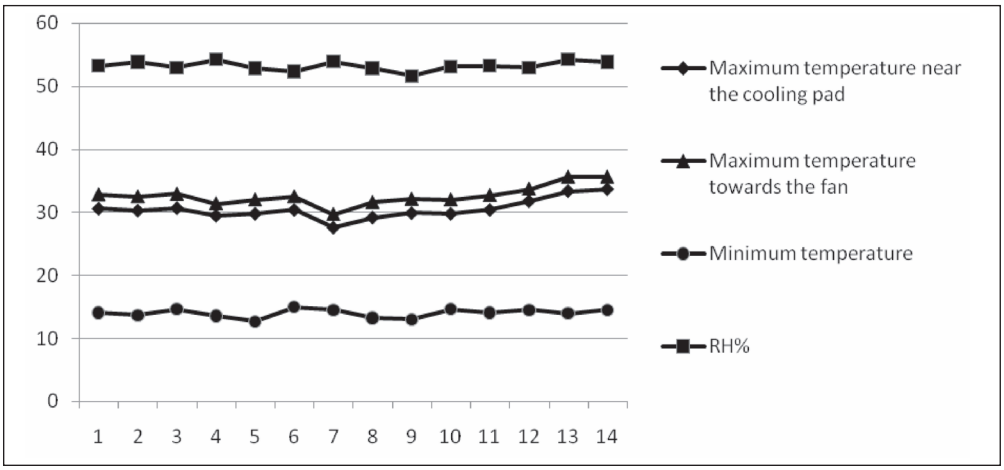

Fig. 1 : Average daytime temperatures, relative humidity (RH) and minimum night temperature inside the greenhouse during the experimental period

temperature from 30.4 to 32.5 °C (Table 1). Significant genotypic differences were observed in net photosynthesis rates at both the temperatures. The commercial hybrid Abhinava and cv. Arka Saurabh showed significantly higher photosynthesis rate in plants exposed to 30.4° C compared to cv. Arka Vikas, 2195 and RF4A. Plants exposed to mild temperature increase of 32.5 °C showed considerable reduction in net photosynthesis rate. However, cv. Arka Saurabh recorded highest photosynthesis rate (15.1 µmol m^{-2} s^{-1}) followed by cv. Arka Vikas and 2195. Among the genotypes, Abhinava showed highest reduction (60%) followed by RF4A (53.55%). Lowest reductions were observed in cv. Arka Vikas (38.6%) followed by 2195 (40%). Further, the reductions in stomatal conductance and transpiration rate were also observed (Table 1). Higher reductions in stomatal conductance were observed in cv. Arka Vikas (95%), 2195 (91.6%) and Abhinava (80%) and lower in cv. Arka Saurabh (62.5%) and RF4A (66.7%). The reduction in transpiration rate was also highest in cv. Arka Vikas (86.9%) followed by Abhinava (66.2%), RF4A (62.3%) and 2195(60.2%). Least reduction was observed in cv. Arka Saurabh (31.4%). The leaf temperatures recorded at the time of measuring photosynthesis rates were higher in the plants exposed to 32.5 °C. Average leaf temperature of 34.6 °C was observed among the genotypes. This could be due to heating of leaves by incoming solar radiation in the TGT and also due to reduction in transpiration rates. Overall the results showed that at peak flowering stage the increase in temperature above the optimal caused reductions in gas exchange characteristics. At this stage, though the net photosynthesis rate was highest in cv. Arka Saurabh at elevated temperature, lowest reductions were observed in cv. Arka Vikas and 2195.

The gas exchange parameters recorded at peak fruiting stage showed marginal reductions due to increase in air temperature from 29.8 to 32.0 °C (Table 2). At 29.8 °C, all the genotypes except 2195 showed photosynthesis rate in the range of 20.5 to 21.9 µmol m^{-2} s^{-1}. Genotype 2195 recorded comparatively lower (18.60 µmol m^{-2} s^{-1}) photosynthesis rate, which is maximum for the genotype in this study. At 32 °C, highest photosynthesis rate was observed in Abhinava and RF4A and cv. Arka Vikas, Arka Saurabh and 2195 showed slightly lower photosynthesis rates. At this stage, though cv. Arka Vikas had 17.6 µmol m^{-2} s^{-1} photosynthesis rate, due to elevated temperature it recorded higher (19.63%) reduction followed by cv. Arka Saurabh (17.07%). Lower reductions were observed in hybrid Abhinava (7.7%), 2195 (10.75%) and RF4A (11.9%), with Abhinava and RF4A maintaining higher photosynthesis rates, 20.3 and 19.3 µmol m^{-2} s^{-1}, respectively. The increase in temperature caused reductions in transpiration rate in all the genotypes (Table 2). Highest reduction was observed in 2195 (40.6%) followed by Arka Vikas (20.57%) and Arka Saurabh (19.05%) and lower reduction in Abhinava (10.75%) and RF4A (12.94%). However, the data on stomatal conductance did not show significant differences due to increase in temperature. Overall, at peak fruiting stage the increase in air temperature

Table 1 : Net photosynthetic rate, stomatal conductance and transpiration rate of five tomato genotypes at peak flowering stage grown at two temperature regimes

Genotypes (G)	Net photosynthetic rate (P_N) (µmol m^{-2} s^{-1})		Stomatal conductance (gs) (mol m^{-2} s^{-1})		Transpiration rate (E) (m mol m^{-2} s^{-1})	
	Treatments (T)					
	30.4 °C	32.5 °C	30.4 °C	32.5 °C	30.4 °C	32.5 °C
Arka Vikas	18.9^{b}	11.6^{b}	4.0^{a}	0.2^{b}	8.4^{a}	1.1^{cd}
Arka Saurabh	26.8^{a}	15.1^{a}	0.8^{b}	0.3^{a}	8.6^{a}	5.9^{a}
Abhinava	25.8^{a}	10.3^{bc}	0.5^{b}	0.1^{c}	7.1^{b}	2.4^{bc}
RF4A	18.3^{b}	08.5^{c}	0.3^{b}	0.1^{c}	5.3^{c}	2.0^{d}
2195	18.5^{b}	11.1^{bc}	2.4^{ab}	0.2^{b}	8.8^{a}	3.5^{b}
Mean	21.7	11.3	1.6	0.2	7.6	3.0
CD at P=0.05						
Treatments (T)	1.330**		1.019**		0.635**	
Genotypes (G)	2.103**		1.612**		1.004**	
TxG	2.974**		1.664*		1.420**	
CV %	8.00		101.14		10.89	

* Significance at P <0.05; ** Significance at P <0.01; Means followed by the same letter in a column do not different significantly according to Duncan's multiple range test

Table 2 : Net photosynthetic rate, stomatal conductance and transpiration rate of five tomato genotypes at peak fruiting stage grown at two temperature regimes

Genotypes (G)	Net photosynthetic rate (P_N) (µmol m^{-2} s^{-1})		Stomatal conductance (gs) (mol m^{-2} s^{-1})		Transpiration rate (E) (m mol m^{-2} s^{-1})	
	Treatments (T)					
	29.8 °C	**32.0 °C**	**29.8 °C**	**32.0 °C**	**29.8 °C**	**32.0 °C**
Arka Vikas	21.9[a]	17.6[b]	1.8[ab]	1.1[b]	8.0[b]	6.4[b]
Arka Saurabh	20.5[a]	17.0[b]	2.0[ab]	1.8[a]	10.5[a]	8.5[a]
Abhinava	22.0[a]	20.3[a]	2.4[a]	1.6[a]	9.3[ab]	8.3[a]
RF4A	21.9[a]	19.3[a]	1.2[b]	1.2[b]	8.5[b]	7.4[ab]
2195	18.6[b]	16.6[b]	2.4[a]	1.7[a]	10.6[a]	6.2[b]
Mean	21.6	17.7	2.0	1.5	9.4	7.4
CD at P=0.05						
Treatments (T)	1.516**		NS		0.860**	
Genotypes (G)	2.397**		0.898*		1.360**	
TxG	NS		NS		1.403*	
CV %	7.56		39.92		9.40	

* Significance at P <0.05; ** Significance at P <0.01; NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test

to 32.0 °C inside the TGT caused marginal reductions in photosynthesis rate compared to peak flowering stage. This marginal reduction in photosynthesis rate at peak fruiting stage could be due to lower increase in average leaf temperature (33.2 °C) among the genotypes at the time of measuring gas exchange characteristics. Previous studies have shown that the increased temperature of 32°C at flowering stage caused reductions not only in photosynthetic rate, but also in leaf conductance and transpiration rate compared to ambient temperature (Islam, 2011). Studies on physiological response of six tomato genotypes to high temperature stress under field and greenhouse conditions showed general reduction in photosynthesis, transpiration and stomatal conductance under temperature stress (Berova *et al*., 2008). In another study, exposing tomato plants to moderately high temperature of 35°C for eight hours caused reduction in photosynthesis rate (Zhang *et al*., 2012). In our study also, reductions in gas exchange characteristics at mild elevated temperature more so at peak flowering stage shows the sensitivity of tomato genotypes to temperatures above the optimal.

Studies on response of tomato genotypes to elevated temperatures have shown the genotypic differences. Evaluation of tomato cultivars under two temperature regimes (37/27 °C or 37/22 °C day/night) showed that the tolerant cultivars showed higher photosynthetic rate under heat stress conditions at different growth stages in comparison to the heat sensitive ones (Abdelmageed and Gruda, 2009). In tomato, Singh *et al*. (2005) observed adverse effect of high temperature on CO_2 gas exchange characteristics and also differential response of four genotypes tested. In the present study also tomato genotypes showed differential response to mild elevated temperatures. Among the genotypes, cv. Arka Vikas and 2195 showed lower reduction in photosynthesis rate as compared to other genotypes at peak flowering stage. The reductions in stomatal conductance and transpiration rate were also higher in these two genotypes. Again at peak fruiting stage, though 2195 recorded photosynthesis rate of 18.60 µmol m^{-2} s^{-1}, the reduction at elevated temperature was lower and highest reduction in transpiration rate was also observed in this genotype.

Chlorophyll fluorescence, an indicator of photochemical efficiency of PSII (Fv/Fm), recorded at both peak flowering and peak fruiting stages, showed overall reduction at elevated temperatures (Table 3). At peak flowering stage reduction was significantly high in cv. Abhinava compared to other genotypes. At peak fruiting stage RF4A showed maximum reduction and no effect was observed in 2195 and least reduction in cv. Arka Vikas. Earlier studies conducted by Camejo *et al*. (2005) also reported the decrease in photochemical efficiency due to higher temperature and plants recovered 20 hours after removing stress conditions. This recovery of PSII indicated that the imposed high temperatures provoked reversible damages on PS II presumably on light harvesting complex. Increase in epicuticular wax content was observed across the genotypes

at elevated temperature (Table 4). However, the differences among the genotypes were not significant. Epicutcular wax is one of the important factors which influences the energy balance of leaf and the amount of epicuticular wax is positively correlated with drought tolerance in peanut (Samdur *et al*., 2003). In a study on wheat genotypes, Mondal, (2011) concluded that the leaf cuticular wax reduces leaf temperature and improves adaptation during high temperature stress. However, in tomato, the genotypic response to increased temperatures in terms of differences in epicuticular wax content needs further investigation.

The leaf total soluble sugars, reducing sugars and proline content increased with increase in temperature at peak fruiting stage (Table 4). Among the genotypes, 2195 recorded the highest total as well as reducing sugars followed by cv.

Table 3 : Chlorophyll fluorescence (photochemical efficiency of PSII) of five tomato genotypes at peak flowering and peak fruiting stages grown at two temperature regimes

	Peak flowering stage		**Peak fruiting stage**	
Genotypes (G)	**Treatments (T)**			
	30.4 °C	**32.5 °C**	**29.8 °C**	**32.0 °C**
Arka Vikas	0.80[a]	0.77[a]	0.77[ab]	0.76[b]
Arka Saurabh	0.78[b]	0.77[a]	0.78[a]	0.75[b]
Abhinava	0.76[c]	0.71[b]	0.79[a]	0.77[a]
RF4A	0.78[b]	0.76[a]	0.79[a]	0.75[b]
2195	0.78[b]	0.77[a]	0.76[b]	0.76[b]
Mean	0.78	0.76	0.78	0.76
CD at P=0.05				
Treatments (T)	0.02**		0.01**	
Genotypes (G)	0.04**		0.02**	
TxG	NS		NS	
CV %	2.91		2.11	

** Significance at P <0.01; NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test

Table 4 : Epicuticular wax content, total soluble sugars, reducing sugars and proline content of five tomato genotypes at peak fruiting stage grown at two temperature regimes

	Epicuticular wax content (µg cm^{-2} fresh leaf)		**Total soluble sugars (mg g^{-1} dry weight of leaf tissue)**		**Reducing sugars (mg g^{-1} dry weight of leaf tissue)**		**Proline (mg g^{-1} dry weight of leaf tissue)**	
Genotypes (G)	**Treatments (T)**							
	29.8 °C	**32.0 °C**	**29.8 °C**	**32.0 °C**	**29.8 °C**	**32.0 °C**	**29.8 °C**	**32.0 °C**
Arka Vikas	73.6[a]	110.1[a]	35.6[a]	58.0[bc]	15.8[b]	43.6[a]	2.5[a]	13.4[a]
Arka Saurabh	78.0[a]	110.0[a]	15.8[d]	67.9[b]	13.1[bc]	21.0[c]	0.7[c]	1.8[d]
Abhinava	60.4[b]	128.9[a]	20.4[c]	54.4[c]	13.9[bc]	33.0[b]	2.9[a]	9.6[b]
RF4A	59.5[b]	82.5[b]	23.2[b]	47.8[d]	10.1[c]	22.7[c]	2.6[b]	4.8[c]
2195	74.0[a]	103.9[a]	26.9[b]	80.7[a]	23.0[a]	46.7[a]	0.7[c]	2.7[cd]
Mean	69.1	107.1	24.4	61.8	15.2	33.4	1.9	6.5
CD at P=0.05								
Treatments (T)	16.83**		3.24**		4.60**		0.68*	
Genotypes (G)	NS		5.12**		7.28**		1.08**	
TxG	NS		7.25**		10.30**		1.53**	
CV %	17.03		12.51		10.35		20.99	

** Significance at P <0.01; NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test

Table 5 : Osmotic potential, osmolytes (total soluble sugars and proline) of five tomato genotypes at fruiting stage grown at two temperature regimes

Genotypes (G)	Leaf osmotic potential; Ψ*s* (-Bars)		Osmolytes (mg g^{-1} dry weight of plant tissue)	
	Treatments (T)			
	29.8 °C	**32.0 °C**	**29.8 °C**	**32.0 °C**
Arka Vikas	12.6[a]	16.1[a]	38.1[a]	71.4[b]
Arka Saurab	11.5[bc]	15.2[b]	16.5[c]	69.7[bc]
Abhinava	13.0[a]	14.7[b]	23.3[b]	64.0[c]
RF4A	11.9[b]	14.6[b]	25.8[b]	52.6[d]
2195	10.9[c]	16.2[a]	27.6[b]	83.4[a]
Mean	12.0	15.4	26.3	68.2
CD at P=0.05				
Treatments (T)	0.29**		12.5*	
Genotype (G)	0.45**		6.78*	
TxG	0.64**		23.45*	
CV %	2.64		12.76	

* Significance at P <0.05; NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test

Arka Saurabh and cv. Arka Vikas, respectively. Lowest total soluble sugars content was observed in RF4A and lowest reducing sugars in cv. Arka Saurabh and RF4A. Among the genotypes, proline content was highest in cv. Arka Vikas followed by Ahinava and lowest in cv. Arka Saurabh. The increase in proline content also contributed to overall osmolytes estimated i.e., total soluble sugars and proline content together. At elevated temperature, highest osmolytes were observed in genotype 2195 followed by cv. Arka Vikas (Table 5). Correspondingly, higher leaf osmotic potential was also observed in these two genotypes (Table 5). The studies on effect of high temperature on carbohydrate metabolism have been conducted in various plant species. In sugarcane, accumulation of soluble sugars under heat stress has been reported by Wahid and Close (2007) with its implications for heat tolerance. Accumulation of osmolytes, including total soluble sugars and proline is an important adaptive mechanism in plants subjected to abiotic stresses as well as temperature extremes (Wahid *et al.,* 2007). In tomato, heat stress perturbed the leaf water relations and root hydraulic conductivity (Morales *et al*., 2003) and under high temperatures, fruit set in tomato plants failed due to the disruption of sugar metabolism and proline transport during male reproductive development (Sato *et al*., 2006). Accumulation of reducing sugars due to increased invertase activities in tomato has been reported (Miguel *et al.,* 2007). However, Zhang *et al,* (2012) reported reduction in reducing sugars concentration and increase in sucrose phosphate synthase activity which caused increase in sucrose content in tomato leaf. In the present study, the results showed the accumulation of both total soluble sugars and reducing sugars in leaf under mild elevated temperature. The higher osmolytes, both total soluble sugars and proline content in leaf estimated at peak fruiting stage caused increase in leaf osmotic potential of genotype 2195 and cv. Arka Vikas under mild elevated temperature.

CONCLUSIONS

The differences in physiological response of five tomato genotypes to elevated temperature in the TGT were evident from the study. Temperatures above optimal caused differential reductions in gas exchange characteristics in five tomato genotypes. Reductions were higher at peak flowering stage compared to peak fruiting stage. Photochemical efficiency of PSII was also reduced at both peak flowering and peak fruiting stages due to increases in temperature. Leaf epicuticular wax content increased across the genotypes at peak fruiting stage and higher total soluble sugars, reducing sugars and proline content contributed to increase in leaf osmotic potential. When the genotypic response in terms of the above parameters was considered, two genotypes, 2195 among the lines and cv. Arka Vikas among the released cultivars performed better under elevated temperatures.

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