DOI : 10.5958/0974-0112.2022.00003.2

Indian J. Hortic. 79(1), March 2022: 15-22

Morphological, biochemical and molecular insights on responses to heat stress in chilli

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ABSTRACT

Four heat susceptible and four heat-tolerant genotypes of chilli were grown under high temperature and control conditions to study the morphological, biochemical and molecular changes occurring in them due to high-temperature stress. It was observed that high temperature did not significantly affect vegetative growth in chilli; however, the reproductive growth was significantly affected and manifested as a reduction in fruit length, width, weight, and number of seeds per fruit. The detrimental effect was pronounced in heat susceptible chilli genotypes. On the other hand, tolerant genotypes accumulated more amounts of protein and proline. In addition, they displayed higher activities of antioxidant enzymes like SOD (superoxide dismutase) and POD (peroxidase) to combat high-temperature stress. Out of seven Capsicum annuum specific heat shock proteins studied, three genes, namely CaHSP 832 (HSP 83), Ca HSP 703(HSP70) and Ca HSP 2272 (small HSP) showed significant differences in expression level between tolerant and susceptible genotypes, thereby suggesting their utility in discriminating the genotypes for their tolerance to heat stress.

Keywords: *Capsicum annuum*, high temperature tolerance, heat shock proteins (HSP), proline content, antioxidant activity

INTRODUCTION

Chilli (*Capsicum annuum* L.), a member of the Solanaceae family, is an important economic crop with a wide variety of uses, including consumable vegetable, condiment in cuisines, pharmaceuticals and colouring agent. Chilli is a warm climate loving crop and shows luxuriant vegetative growth at high temperature, however when temperature goes above 40°C, the crop fails to set fruit. In chilli, flower abscission is high if day temperature is in the range of 32-38°C, whereas fruit retention is maximam at 16-21°C day temperature (Demers *et al*., 3). India is a tropical country and northern India experiences very high temperatures during the summer season. Therefore, in order to have a spring summer crop especially in northern India, it is important that the varieties grown in this season are able to tolerate the high temperature during April to July (which may go even beyond 40°C). High temperature affects percent fruit set, size of fruits as well as wide spectrum of both biochemical and physiological responses within the plant cells (Saha *et al*., 18). Heat stress inhibits chilli seed vigor, reduces chlorophyll content of leaves that results in lower photosynthesis rate, finally resulting in fertilization failure, flower and fruit dropping (Erickson and Markhart, 5).

A few heat tolerant chilli genotypes have been identified at ICAR-IARI, New Delhi. These lines have given consistent fruit yield during hot summer conditions of New Delhi when most of the other genotypes failed to set fruits. This necessitates further studies to ascertain the mechanism of heat tolerance in these genotypes. An in-depth comparative analysis of the morphological, biochemical and molecular responses of chilli genotypes with contrasting heat tolerance attributes was aimed at in the present investigations.

MATERIALS AND METHODS

Four heat tolerant genotypes of chilli (*Capsicum annuum* L.) were chosen which had different fruit bearing habit and fruit characteristics but had shown successful fruit setting at high temperatures consecutively for three years (2014-15 to 2016-17), isolated and fixed. The heat tolerant genotypes selected were DLS-161-1, DLS-10-2 (both highly tolerant) and DLS-152-1, DLS-20-11 (both moderately tolerant) while the susceptible genotypes were Chilli Kashmir long (CKL), Jwalamukhi, Anugraha and Pusa Jwala. The test genotypes were grown under both ambient temperature condition (ATC) and natural field conditions (high temperature condition (HTC)). For ambient condition, the plants were raised in temperature controlled greenhouse facilities where temperature was maintained at 15+2°C (night) and 27+3°C (day) for 8 hrs and 16 hrs, respectively. Summer season (May-June) was used to study test genotypes under HTC at New

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Delhi. Sowing of the test genotypes was done in the last week of February, 2018 and seedlings were transplanted into mud pots 40 days after sowing. Vegetative stage lasted for 55 to 65 days after transplanting i.e., till 30th May, 2018 in different genotypes and reproductive stage was observed during the month of June under both ATC and HTC.

The test genotypes were grown in four sets and each set consisted of thirty plants. Two sets each were grown under ATC and HTC. One set of genotypes raised under ATC was used for comparing vegetative stage characters whereas HTC temperature condition (Table 1.).

At vegetative stage, data were recorded on growth characters like number of branches and plant height. At reproductive stage, data were recorded on days to 50% flowering, fruit length, fruit width, fruit weight, number of fruits per plant and number of seeds per fruit. Biochemical characters like protein content, lipid peroxidation (malondialdehyde content), activities of enzymes like superoxide dismutase, guaiacol peroxidase and proline accumulation were estimated. Thirty plants in each set were divided into three replications with ten plants per replication. Five plants from each replication were chosen at random for recording the observations. Data on various observations were recorded and leaf samples for conducting various biochemical tests were harvested in June when the plants entered the reproductive phase.

The protein accumulation was estimated using the protocol of Bradford (2). The level of lipid peroxidation (Malondialdehyde assay) was measured in terms of TBARS content as per Heath and Packer (10). Proline content was determined according to method of Bates *et al*. (1) with modification. Superoxide dismutase (SOD) activity was determined in crude extract by measuring its ability to inhibit the photochemical reduction of nitro-blue tetrazolium (NBT) in the presence of riboflavin in light (Giannopolitis and Ries, 7). One unit of enzyme activity was determined as the amount of the enzyme needed for the inhibition of 50% NBT reduction rate by monitoring absorbance at 560 nm with spectrophotometer. Activity of guaiacol-peroxidase (GP) was determined following the method of Evers *et al*. (6). The amount of H_2O_2 was quantified as described by Loreto and Velikova (14) and expressed as µmol/g fresh weight (FW).

The expression of seven different heat shock protein genes belonging to different molecular weight classes viz. HSP83 (denoted by CaHSP83), HSP 70 (denoted by CaHSP703), HSP 90 (denoted by CaHSP90), small molecular weight HSP denoted by CaHSP3, CaHSP2272 and CaHSP2271(both CaHSP2272 and CaHSP2271 of 22.7 KDa) and chloroplastic HSP denoted by CaCHSP was studied during the present investigation. Nomenclature used for naming the genes used in present investigation is the same used by Li *et al*. (13) and already published primers sequences of these genes by Li *et al*. (13) were used for the study. Leaf samples were collected from the test genotypes in the month of June, 2018 in liquid N_2 and stored in deep freezer (-80°C) until RNA isolation. Three biological replicates were collected from each line.

RNA extraction and gene expression studies were carried out as per the protocol of Mangal *et al*. (15). The ΔCt of each target gene was normalized with internal control Ubiquitin (Hongjian *et al*., 11). The ΔΔCt values were calculated taking ΔCt of Chilli kashmiri long as calibrator and were used to plot graph to study the relative expression of each gene in the genotypes under study. Results reported in this paper are mean values with their standard deviations obtained from three independent replications. Morphological and biochemical data were analyzed for complete randomized design (CRD) using Online Agriculture Data Analysis Tool, OPSTAT.

RESULTS AND DISCUSSION

Data presented in table 2 show variations in various morphological parameters in different genotypes under study at ATC and HTC including the per cent change in values of different morphological traits under HTC over ATC. It is clear from Table 2 that number of primary branches and plant height increased in all the genotypes under HTC while all the other traits showed lower values when plants were exposed to high temperature. Per cent change in traits like number of primary branches (except CKL), plant height,

Table 1. Temperature regimes maintained for ambient and heat stress conditions

Stage	Temperature under ambient conditions	Temperature under natural field conditions (heat stress)
Vegetative stage	maximum and minimum temp of 30-32°C and 20-23°C, respectively	maximum and minimum temp of 35-44°C and 25-30°C, respectively
Reproductive stage	maximum and minimum temp of 30-32°C and 20-23°C, respectively	maximum and minimum temp of 37-42°C and 26-34°C, respectively

Table 2: Mean performance of test genotypes under ambient (Amb) and high temperature (HT) conditions:

Genotype	No. of primary branches			Plant height (PH)			Days to 50% flowering			Fruit length (FL)			Fruit width (FW)			Fruit weight (AFW)			Number of fruits per plant			Number of seeds per fruit		
	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C	Amb	HT	% C
CKL	3.3	4.6	38.1↑	60.6	64.0	5.6↑	64.3	59.0	8.3↓	5.5	4.6	15.4↓	2.1	1.9	8.2↓	2.9	2.4	18.1↓	19.7	5.3	72.9↓	17.7	0.3	98.1↓
Jwalamukhi	3.8	4.3	13.9↑	63.7	69.0	8.4↑	56.7	52.3	7.7↓	7.9	6.5	17.7↓	1.5	1.3	16.4↓	2.7	2.0	25.2↓	26.7	5.0	81.3↓	28.3	0.3	98.8↓
Anugraha	4.7	5.1	9.2↑	54.3	58.0	6.8↑	51.3	47.0	8.4↓	6.8	5.8	15.1↓	1.1	0.7	37.3↓	1.8	1.4	25.1↓	34.3	9.7	71.8↓	37.3	3.0	92.0↓
Pusa Jwala	4.0	4.0	0.8↑	45.3	47.0	3.7↑	56.7	52.0	8.2↓	8.9	7.2	18.8↓	1.0	0.6	41.2↓	1.8	1.2	32.0↓	19.0	5.0	73.7↓	35.3	0.7	98.1↓
DLS-161-1	3.6	4.0	13.1↑	37.3	39.7	6.3↑	64.0	58.3	8.9↓	5.9	5.2	12.3↓	1.2	0.6	50.0↓	1.5	1.2	21.6↓	35.0	33.3	4.8↓	38.0	19.0	50.0↓
DLS-10-02	3.9	4.6	17.2↑	35.7	37.7	5.6↑	60.3	58.0	3.9↓	6.1	5.5	8.9↓	0.9	0.6	39.8↓	1.3	0.98	26.3↓	35.7	29.0	18.7↓	35.0	15.0	57.1↓
DLS-20-11	3.3	3.4	2.1↑	38.7	38.7	0.0↑	60.7	56.3	7.2↓	6.3	5.7	10.0↓	1.0	0.6	41.0↓	1.2	1.0	19.4↓	31.0	22.3	28.0↓	37.0	14.0	62.2↓
DLS-152-1	3.4	3.9	16.6↑	42.0	43.0	2.4↑	63.3	57.3	9.5↓	6.1	5.5	8.9↓	1.2	0.6	45.2↓	1.4	1.2	19.0↓	27.3	23.3	14.6↓	34.0	11.3	67.1↓
C.D.	N/A	0.6		3.6	2.1		3.5	2.08		0.5	0.3		0.1	0.1		0.2	0.15		3.5	3.6		5.5	2.1	
SE(m)	0.32	0.2		1.2	0.7		1.2	0.69		0.2	0.1		0.03	0.04		0.07	0.05		1.2	1.2		1.8	0.7	
SE(d)	0.45	0.3		1.7	1.0		1.6	0.97		0.2	0.1		0.04	0.06		0.09	0.07		1.6	1.7		2.6	0.97	
C.V. (%)	14.7	7.5		4.35	2.47		3.4	2.16		4.5	2.7		3.9	8.8		6.2	6.1		6.96	12.5		9.7	14.9	

PH in cm; FL in cm, FW in cm, AFW in g, FYP in g; %C: Per cent change, ↓: Decrease, ↑: Increase

N/A: Not applicable as data is showing non signicant differences between genotypes

days to 50% flowering (except CKL) and fruit length between tolerant and susceptible genotypes under ATC and HTC were not significant. However, there was significant reduction in the yield contributing traits like number of fruit per plant and number of seeds per fruit in all the heat susceptible genotypes under HTC as compared to heat tolerant genotypes.

The most important observation among these parameters was that the percent decline in two important yield contributing traits namely number of fruits per plant and number of seeds per fruit was much less in heat tolerant genotypes under HTC as compared to heat susceptible genotypes under heat stress conditions. Number of seeds per fruit also reduced drastically in the fruits set in susceptible genotypes under HTC. Most of the seeds turned brown and were shriveled under HTC (**Plate 1**). The genotype DLS-161-1 showed the best performance with respect to yield attributing traits among all the tested genotypes under HTC.

On studying the biochemical parameters between the heat susceptible and heat tolerant genotypes

Plate 1: Seed set in fruits of A-161-1 (A: At ambient temperature, B: At High temperature) and Anugraha (C: At ambient temperature, D: At High temperature)

under HTC, it was found that there was significant difference between the two groups for protein content, enzyme activities like SOD and GPX, proline content and MDA content (**Fig. 1A-E**). Protein content and proline accumulation was higher in heat tolerant genotypes along with higher SOD and GPX activities in comparison to heat susceptible genotypes. MDA content representing lipid peroxidation was lower in heat tolerant genotypes when compared with heat susceptible.

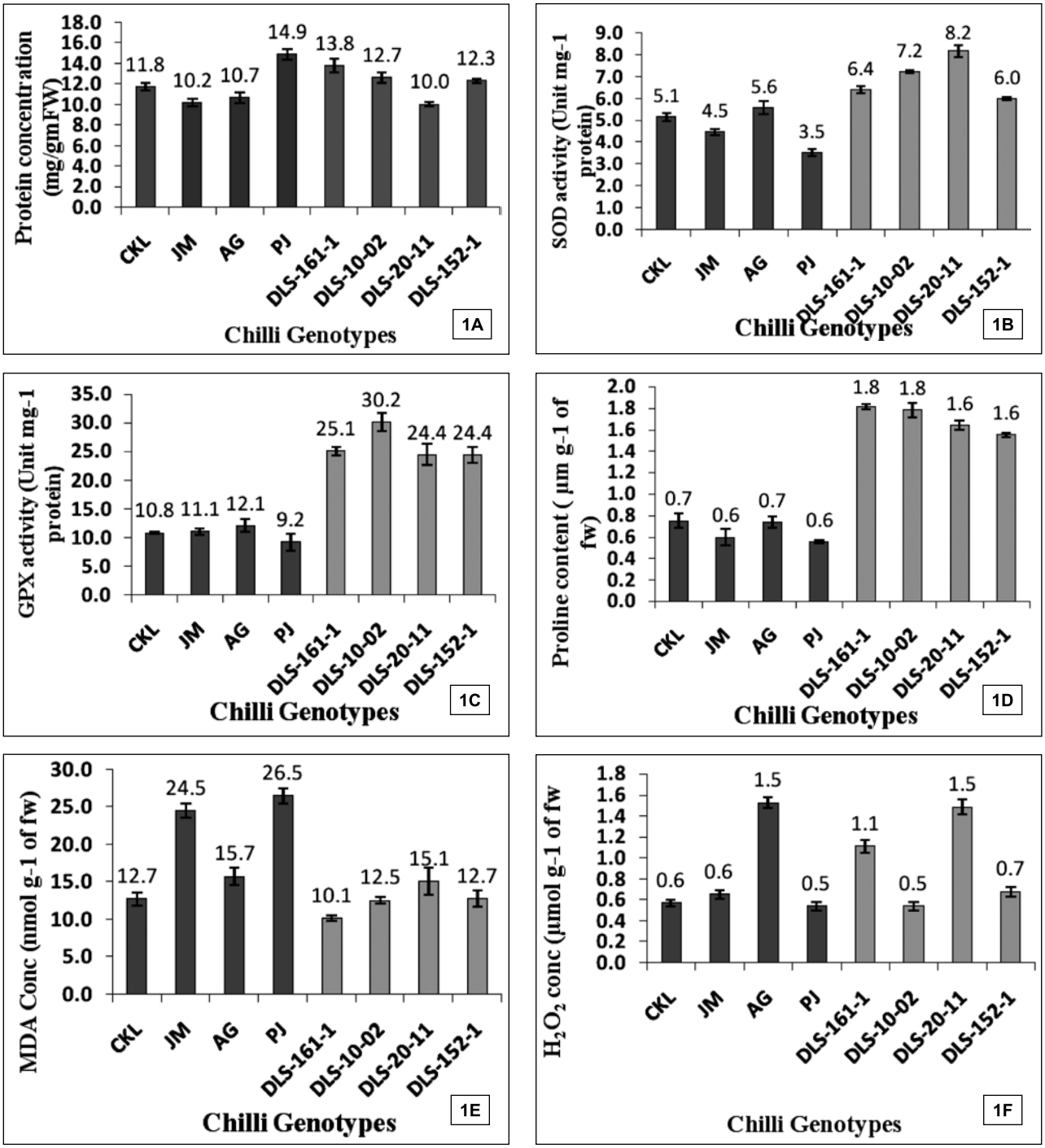

Fig. 1. Comparison between different genotypes for biochemical attributes under high temperature conditions

*CKL-Chilli Kashmiri long, JM-Jwalamukhi, Ag-Anugraha, PJ-Pusa Jwala

Fig 2(A-G) clearly demonstrates that the four heat tolerant genotypes exhibited higher expression of Ca HSP 832, CaHSP 703 as well as of Ca HSP 2272 , in addition the level of up regulation of these genes in different heat tolerant genotypes also showed variations. Relative expression of Ca HSP 832 was found to be the higher in DLS-10-02 followed by DLS-20-11 (whereas the expression of CaHSP 703 was the highest in DLS-161-1 (5.4 folds) followed by DLS-20-1 (4.4 folds). Out of the two lines with highest up regulation of Ca HSP 832 and CaHSP 703, one belonged to highly tolerant class while the other to the moderately tolerant class. In case of Ca HSP 90 gene, although both the highly tolerant lines (DLS-161-1 and DLS-10-02) were among the three genotypes showing the highest expression (in the range of 2.0-2.9 folds), however moderately tolerant lines showed the lowest expression while three of the susceptible lines showed medium level of expression and one of the susceptible line was among the three lines showing the highest expression. Similar results were observed in case of Ca HSP3, Ca HSP 2271 and Ca CHSP genes where although highly tolerant lines showed the highest expression but there was not much difference between the expression in moderately tolerant or heat susceptible lines. All the heat tolerant genotypes (irrespective of their level of heat tolerance) showed higher expression of Ca HSP2272 as compared to heat susceptible genotypes and the minimum difference between the expression of this gene between tolerant and susceptible lines was 4.8 fold while the highest difference was 26.1 folds.

Rising global temperature due to climate change is a subject of importance to the field of agriculture as it has been found to have a significant effect on plant growth, development and productivity. Increase in temperature for a given period of time is called heat stress and this elicits different responses across plant species depending on the stage of development at which it occurs and also the duration of occurrence.

Out of the various morphological traits studied, number of branches and plant height were least affected due to high temperature stress in both the heat susceptible and tolerant genotypes. Though both the groups registered increase in number of branches and plant height but the difference in increase was not significant. Studies have shown that high temperature favours plant growth in chilli analogous to our results (Guo *et al*., 8). High temperature does not distress plant growth at vegetative stage if proper irrigation and fertilization is applied. Photosynthesis and nitrate concentration increase under high temperatures manifesting better vegetative performance as a result of better carbon fixation and storage. Days to 50% plant flowering after transplanting indicate the earliness of the genotype to complete its life cycle which differed significantly among the genotypes studied. It was observed that all the genotypes flowered early under heat stress. Increase in temperature due to climate change results in early flowering in crops and other plants (Jagdeesh *et al*., 12). Field-based experiments where temperature was increased artificially exposing wheat plants to high temperatures resulted in significant early heading (White *et al*., 20).

Majority of studies on heat stress indicate that reproductive stage is more sensitive to high temperature than vegetative stage. In present studies, this was manifested as reduction in fruit length, fruit width, fruit weight, number of fruits per plant and number of seeds per fruit in both heat susceptible and heat tolerant genotypes but the decrease in susceptible genotypes was very high in comparison to tolerant ones. This is in complete agreement with the results of Pagamas and Nawata (16) who reported that applying heat stress after anthesis in chilli results in significant decrease in fruit width, fruit length, fruit weight and seed set. Heat stress after anthesis also increased the proportion of abnormal seeds which has also been observed in the present study. The major reason for low fruit setting is reduction in pollen viability which results in decrease in fruit size *viz*., length and width and fruit set. There are many reports of reduced fruit yield in solanaceous crops including tomato, chilli and brinjal (Pagamas and Nawata, 16; Xu *et al*., 21). The heat tolerant genotypes in our study have manifested good number of fruit set with viable seeds in comparison to the susceptible genotypes.

It has been reported that there is decrease in normal protein synthesis under high temperature conditions (Gurley and Key, 9). There are also several reports indicating positive correlation between proline accumulation and ability of plants to handle environmental stress. Increase in level of proline (an excellent osmolyte) helps to maintain turgor pressure thereby stabilizing cell membranes by preventing electrolyte leakage (Smirnoff *et al*., 19). In the present study, protein and proline content in susceptible genotypes was significantly less than the tolerant genotypes under heat stress.

Heat stress causes oxidative stress which is marked by the generation of reactive oxygen species (ROS). An important protection of cell membrane is catalysed by superoxide dismutase (SOD) where superoxide anion is converted to O_2 and H_2O_2. Similarly, guaiacol peroxidases (GPX), located in cytosol, vacuole, cell wall and apoplast, are also

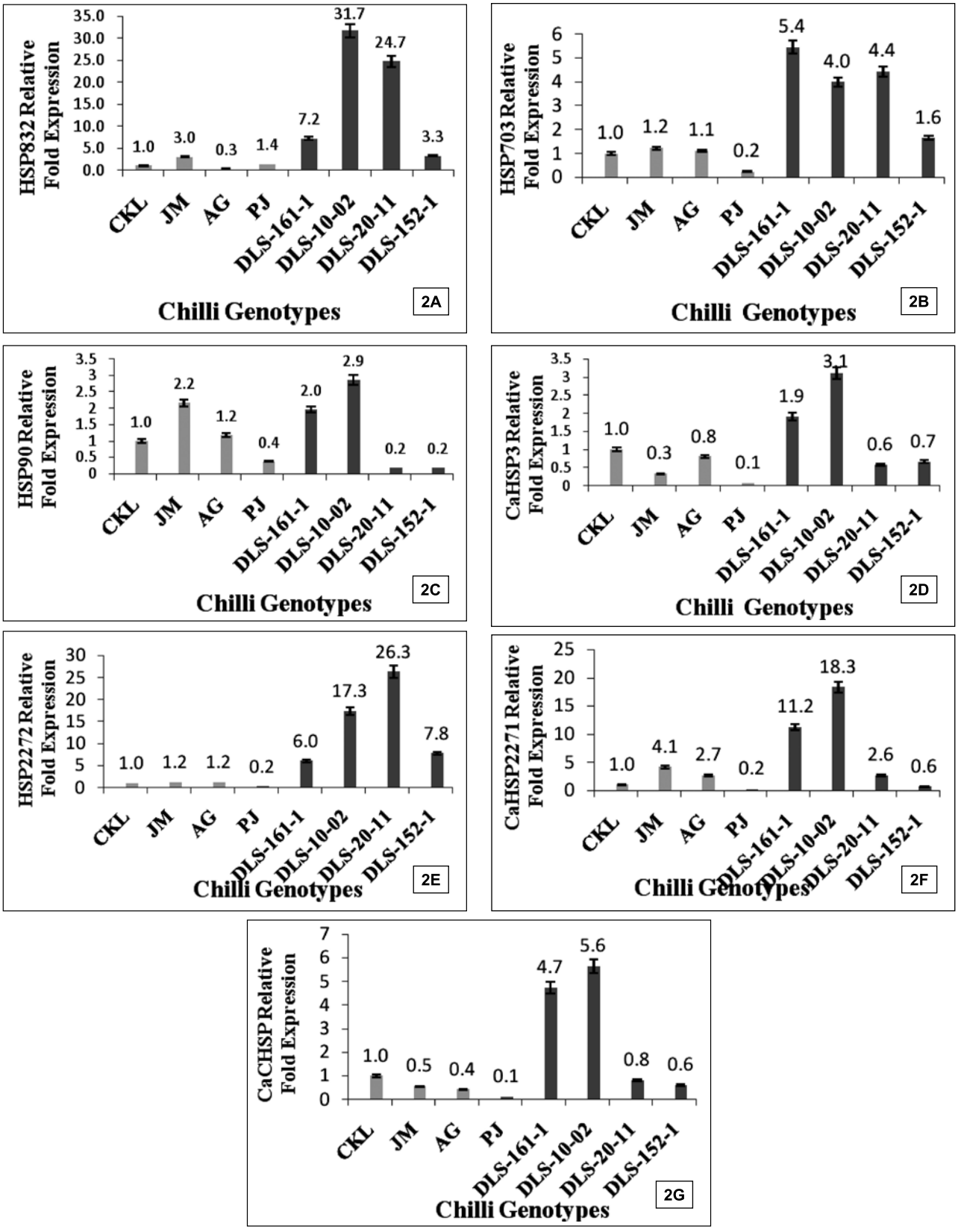

Fig. 2. Relative expression of different heat shock protein genes in heat susceptible and tolerant genotypes

assumed to be involved in ROS scavenging (Jebara *et al*, 13). Studies have shown that tolerance to high temperature stress is associated with increase in levels of antioxidant enzymes like SOD and GPX. Persistent level of high amount of SOD and POD activity in our heat tolerant genotypes in comparison to the susceptible genotype suggests their role in imparting heat tolerance to DLS-161-1, DLS-10-02, DLS-20-11 and DLS-152-1 genotypes.

Lipid peroxidation, protein denaturation and DNA mutation are caused when ROS reacts with lipids, proteins and nucleic acid. High temperature increases leaf temperature which reduces the antioxidant enzyme activities and this in turn increases the level of malondialdehyde (MDA) content in leaves (Djanaguiraman *et al*., 4). The heat tolerant genotypes in our study manifested lower levels of MDA content indicating high antioxidant activity and lower amount of lipid peroxidation, thus displaying better protective mechanisms against heat. We observed that the level of H_2O_2 was not different among the heat susceptible and heat tolerant genotypes, so we assume that better ability of heat tolerant genotypes to deal with heat stress in spite of H_2O_2 production may be attributed to expression of other biochemical compounds and enzymes which lead to mitigation of damage in tolerant genotypes.

One of the major implications of heat stress in plants is the disruption and denaturation of proteins due to improper folding of their constituent linear amino acid chains which results in unfavourable interactions or protein aggregation. Plants control this protein disruption by utilizing heat stress proteins or molecular chaperone to maintain high quality proteins in the cell. In order to counteract the damage by heat stress, plants increase the level of pre-existing HSPs and also express additional HSPs through signalling mechanism (Reddy *et al*., 17). During the present investigations, expression of seven heat shock proteins was studied in the test genotypes. When the performance of heat susceptible lines was compared with the heat tolerant lines (irrespective of tolerance level), three genes namely CaHSP 832 (HSP 83), CaHSP 703 (HSP70) and CaHSP 2272 (small HSP) showed significant difference in the expression level. Out of these three genes, CaHSP 703 (HSP 70) showed highly significant differences in expression between susceptible lines and tolerant lines. However, when the comparison of expression level was made between susceptible and highly heat tolerant lines (DLS-161-1 and DLS-10-02), all the HSP genes studied except CaHSP 90 showed significant differences in the expression level suggesting thereby their utility in discriminating the genotypes for their tolerance to heat stress. Thus the present study highlights the role of different HSPs in adaptability of chilli plants to heat stress. Present results also indicate that HSP 70 is playing the most significant role in chill plant's tolerance to heat stress as it showed significant differences in expression between all tolerant and susceptible lines, while HSP 90 may not be playing a significant role here as its expression was found to be at par even in the highly tolerant and most susceptible lines. Similar observations were made by Li *et al*. (13) regarding HSP 70 in chilli.

AUTHORS' CONTRIBUTION

Conceptualization (AS, MM); Designing of the experiments (AS, MM); Contribution of experimental materials (AS); Execution of field/lab experiments and data collection (KS, BRP); Analysis of data and interpretation (AS,MM, AK, BST); Preparation of the manuscript (AS,MM, AK, BST)

DECLARATION

The authors declare that there is no conflict of interest

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Received : January, 2022; Revised : March, 2022; Accepted : March, 2022