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Study of heat stress memory related to acquired thermo-tolerance in wheat

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ABSTRACT

Wheat is one of the important plants frequently suffer by effects of heat stress. In the present study, heat priming for the first generation studied on heat tolerance of the successive generations in seedling and maturity stages under high temperature stress. Under high-temperature stress condition during seedling stage, the progeny of heat-primed (PH) genotypes shown significantly higher chlorophyll a and b content and percent tetrazolium chloride (%TTC) reduction than the progeny of the non-heat primed (NH) genotypes. At maturity stage, higher grain yield per plant was obtained for PH genotypes than NH genotypes under heat stress condition, which was mainly associated with the higher grain weight for PH than NH genotypes. The greater grain weight could be resulted from the higher percent cell membrane thermo-stability (%CMS) in the PH genotypes than in the NH genotypes. Estimation of variance components and broad sense heritability were higher in PH genotypes than observed in NH genotypes for most studied traits at seedling and maturity stages. Based on morpho-physiological traits, the highest genetic distance was recorded between G9 genotype of heat-primed plants and G9 genotype of non-primed plants, which gave highly significant differences between PH plants and NH plants for all studied traits. The heat priming for the parents may induce heat tolerance for offspring, and this might be an effective method to cope with severe heat stress during some the different growth stages in wheat.

KEYWORDS: Wheat, Heat stress, Epigenetics, Stress memory.

1. INTRODUCTION

The worldwide is used wheat as staple food. However, grain yield of wheat decreases largely under biotic and abiotic stresses. With climate change of the global, the occurrences of extreme weather events such as drought and heat stresses have significantly increased, in terms of frequency, duration and extent (Field *et al*. 2014). The optimum temperature of growth in wheat is around 21°C during reproductive growth (Porter and Gawith 1999). During grain filling, wheat plants are high sensitive to high temperature stress. Heat priming for the parent was studied on tolerance of the progeny of parents in post-anthesis under high temperature stress (Wang *et al*. 2016). Pre-exposure of plants to moderate stress may bring about "stress memory" that helps a fast protective response to next stress event (Boyko and Kovalchuk 2011). Stress memory has been defined as physiological, genetic and epigenetic changes under stress conditions, and it modifies responses to reoccurring stress in the same generation or in the next generation. (Boyko and Kovalchuk 2011). Stress memory in the same generation has been found to be correlated with increased tolerance to several abiotic or biotic stresses in many species of plants (Conrath *et al*. 2006). Molecular analysis displays that stress memory induced by pathogen attack (Conrath 2011), are associated with epigenetic variations (such as chromatin remodeling, DNA methylation, or small interfering RNAs), chromatin modifications, signaling proteins accumulation, and primary of metabolism alterations (Conrath 2011).

Hsieh et al. (2009) reported that a general mechanism supposed to restrict transmission of acquired epigenetic states between generations includes establishing of a default epigenetic status during gametogenesis and early phases of embryo development. Previous studies have appeared that mid-heat priming applied before anthesis effectively decreased the impacts of serious high temperature stress occurring during grain filling. This reduction was attributed to diminished damage by sub-cellular levels and oxidative stress at leaf, and thus a large maintenance of photosynthesis (Wang et al. 2011; 2014), and to enhanced carbohydrate remobilization from stems to grains (Wang et al. 2012). The primed

heat treatment induces improving tolerance to stress reoccurring in the next generation (Rasmann et al. 2012). The researches in the future are needed to confirm the molecular mechanisms in which plant store information during stress exposure because biotic and abiotic stresses limit agricultural production and stress responses often lead to down-regulation of yield determining processes such as photosynthesis.

The current study aims to, (1): Impacts of the pre-exposure to heat stress on heat tolerance induced in the next generations. (2): Determine to the situation of several physiological and morphological traits at seedling and maturity stages under heat stress condition in progeny of heat exposure plants from flowering to maturity stages compared to progeny of non-heat prepared plants.

2. MATERIALS AND MTHODS

2.1. The plant material and heat stress priming:

The initial plant material used in the present study consisted of seven genotypes of bread wheat (*Triticum aestivum* L.) and three genotypes of durum wheat (*Triticum durum* L.) in Table 1, were varied in their yield performance under heat stress**.** The field treatment was carried out at the Experimental Farm of Faculty of Agriculture, Assiut University, Egypt. In 2016/2017 winter season, seeds of the ten genotypes were planted on 21st November as an optimal sowing date (non-primed genotypes, NH) and 21st January as a late sowing date (heat primed genotypes, PH) to expose genotypes to high temperatures from inception of the flowering stage. At maturity, seeds from both sowing dates were harvested.

Table 1. Pedigree of durum and bread wheat genotypes used in the study.

	Name	Code	Pedigree
Durum wheat	BANI SEWEF 1	G1	JO"S"/AA"S"/FG"S"
	SVEVO	G2	Cimmyt's Line / Zenit
	WK-12	G3	The landraces were originally collected from farmers' fields near Dandara Temple at Qena Governorate in 1993 (Omara, 1994) and were grown since then every year in order to ascertain the stability of the black glume character.
Bread wheat	GIZA 168	G4	MIL/BUC//SERI
	L.S.15 (Long spike 15)	G5	An advanced long-spike inbred line (F14) derived from a cross among landraces collected from stress areas in Upper Egypt (Omara,1994)
	Sonora 64	G6	YAKTANA-54//NORIN-10/BREVOR/3/2*YAQUI-54
	Line 6	G7	Advanced long spike, short statured inbred line derived from a cross between two landraces collected from dry areas in Upper Egypt (Omara, 1994)
	L.S.16 (Long spike 16)	G8	An advanced long-spike inbred line (F14) derived from a cross among landraces collected from stress areas in Upper Egypt (Omara,1994)
	1*15	G9	Advanced breeding line derived from inter population-interenvironmental cross between early segregates selected in two contrasting environments
	SIDS 1	G10	HD2173/PAVON"S"//1158.57/MAYA 74 "S"

2.2. Estimate of morpho-phosiological traits at seedling stage:

Seeds harvested from each genotype in optimal and lates sowing date were divided into two groups: The first group was sown in high temperature environment in incubation at a day/night temperature of 35-37°C, includes the seeds of each genotype yielded under the optimal (non-priming heat stress, NH) and late sowing date (priming heat stress, PH) conditions. The second group was sown in optimal temperature at 20±2°C, includes the seeds of each genotype obtained under the optimal (non-priming heat stress, NC) and late sowing date (priming heat stress, PC) conditions. In both two experiments, the seeds of each genotype generated under optimal and late sowing date, were immersed in sodium hypochlorite for 5 min, then washed three times with distilled water and allowed to germinate in aluminum trays of 30 cm wide × 60 cm long × 7 cm deep, which were filled with sterilized sand with depth of 5 cm. All experiments were conducted in a randomized complete block design with three replicates in a growth chamber under dark conditions for the first three days. Seedlings were harvested at the 10th day and separated from the remaining seeds. Growth parameters at seedling stage namely; % of germination (%G), shoot length, cm (Sh.L) and root length, cm (R.L), were measured on 10 plants per replicate for each genotype within each group (NH, PH, NC and PC) as well as chlorophyll a and b contents (Chl a,b) and percent tetrazolium chloride reduction (%TTC) were estimated.

2.3. Tetrazolium chloride (%TTC) reduction and chlorophyll a, b content (Chl a,b):

Both %TTC and Chl a, b measurements were measured on individual plant bases. From each genotype within each group, 10 plants were evaluated for %TTC reduction using the method of Ibrahim and Quick (2001). The level of acquired high temperature tolerance was determined by measuring the percentage reduction of TTC to formazan using the following

formula: %TTC = (ODh / ODc) × 100
where, ODh refers to the mean optical density (530 nm) values for the heat-stressed set (49 °C for 90 min), and ODc refers to the mean optical density for the control set (25 °C for 90 min).
Chlorophyll a and b content was estimated following the method of Arnon (1949).

2.4. Estimate of morpho-physiological traits at flowering and maturity stage:

In 2017/2018 season, the seeds harvested from each genotype in optimal and late sowing date were divided into two groups: The first group was sown in optimal (20 November, control) and second group was sown in late (20 January, heat stress) sowing date in the Farm of Faculty of Agriculture, Assiut University, Egypt. Both experiments were included on the seeds of each genotype generated under the optimal (NH) and late sowing date (PH) conditions. The experimental design was RCBD in three replications. Each wheat genotype was represented in each block by a row of 10 plants spaced 25 cm apart within rows set 30 cm from each other. At flowering stage, relative water content (RWC) and the percent of cell membrane thermo-stability (%CMS) were estimated. In addition, grain yield per plant (g) and 1000 grain weight (g) were measured at the maturity stage in the two sowing dates. Relative water content (%) was calculated using the formula proposed by Ritchier *et al.* (1990). Cell membrane thermo-stability (%CMS) assay was performed according to the method described by Fokar *et al.* (1998).

The recorded maximum air temperatures at the experimental site during March and April of the three consecutive seasons are illustrated graphically in Figure 1 (weather reports in Assiut, https//: W under ground.com) several waves of heat (>34 C°) characterized the weather of March whereas stronger heat waves (>38 C°) prevailed during April especially in 2017 and 2018 which coincided with the pre-flowering stage.

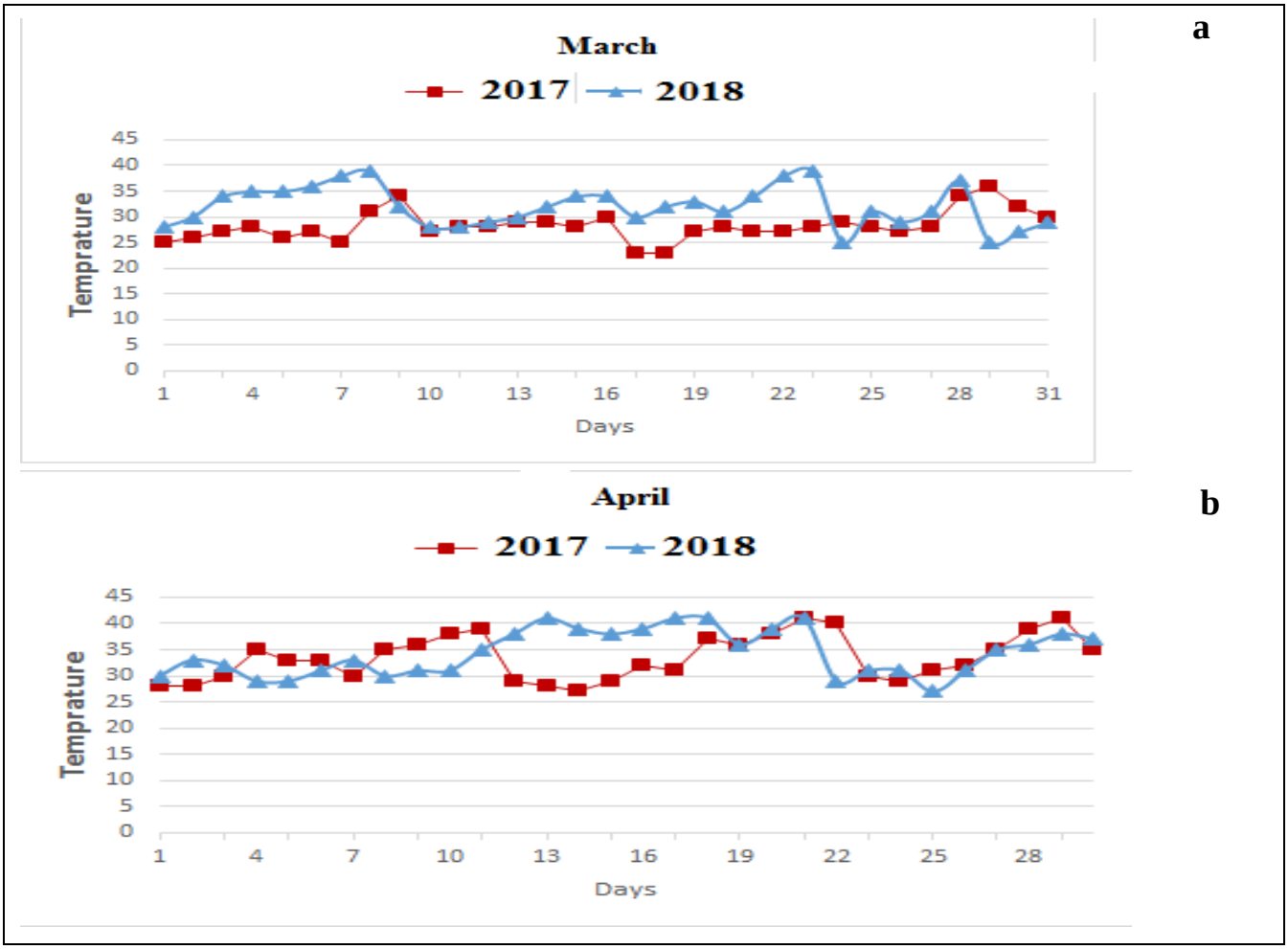

Fig. 1. The recorded maximum air temperature at the experimental site in March (a) and April (b) of the two seasons 2017 and 2018.

2.5. Phenotypic data analysis:

Significantly different means of the results were separated at $P < 0.05$ by Fisher's Least Significant Difference (LSD) and Duncan's multiple range test. Combined analyses of variances across control and heat stress environments and between priming heat (P) and non-priming (N) were used, the broad-sense heritability (h^2B) was estimated using the combined analyses of variances between control and heat stress for each separated group of genotypes primed and non-primed. The broad-sense heritability of a trait was computed using the formula described by Nyquist (1991). T-test was used to significant differences showing between primed plants and non-primed plants for each genotype.

3. RESULTS

3.1. Progeny performance of heat primed and non-primed genotypes at seedling stage:

Progeny means of heat primed and non-primed genotypes under control and heat stress are presented in Table 2. Shoot length ranged from 7.13 (G1) to 17.68 (G9) with an average of 13.12 (cm) in progeny of heat primed plants under heat stress (PH) conditions. Furthermore, the shoot length values extended from 10.12 (G6) to 16.40 (G9) with an average of 12.88 cm in progeny of non-heat primed genotypes under heat stress (NH). As well as, the reduction in shoot length due to heat stress was 19.90% in the progeny of PH genotypes compared to 23.79% in the progeny of NH genotypes. The chlorophyll a content ranged from 3.87 (G6) to 11.11 (G9) with an average of 6.97 μgg^{-1} in the progeny of PH genotypes, whereas in the progeny of NH genotypes it ranged from 3.42 (G5) to 9.28 (G4) with an average of 6.23 μgg^{-1} while, chlorophyll b content decreased in the progeny of NH genotypes (6.58%) than in the progeny of PH genotypes (6.13%) under heat stress condition. The progeny of PH genotypes showed a %TTC reduction from 28.21% (G7) to78.40% (G9) with an average of 64.08%. Moreover, the % TTC reduction in progeny of NH genotypes extended from 37.28% (G7) to 66.80% (G8) with an average of 51.94%. Under heat stress condition, the amount of % TTC reduction increased amount of (29.69%) in progeny of PH genotypes, whereas it increased by 26.59% in the progeny of NH genotypes. But the high increase of %TTC reduction was obtained for progeny of PH which amounted to 56.18% compared with the progeny of NC genotypes, indicating that the increase due to effects of environmental epigenetics and inherited epigenetically.

3.2. Progeny performance of heat primed and non-primed genotypes at maturity stage:

Progeny means of heat primed and non-primed plants under both favorable and heat stress conditions were shown in Table 3. The percent of cell membrane thermo-stability (%CMS) mean values ranged from 21.99 (G10) to 58.28% (G9) with an average of 41.91% in progeny of NH genotypes, while in progeny of PH genotypes extended from 22.41 (G7) to 81.47% (G9) with an average of 48.01%.

The % CMS in progeny of PH genotypes increased by 14.56% more than the progeny of NH genotypes. In the progeny of PH genotypes, grain yield per plant extended from 21.18 (G1) to 48.89 g (G3) with an average of 33.21g, whereas the 1000 grain weight ranged from 38.93 (G4) to 50.53 g (G2) with an average overall of 44.72 g. The grain yield per plant and 1000 grain weight decreased by 55.62 and 10.15%, respectively, in progeny of PH genotypes compared with 62.73 and 11.635% in the progeny of NH genotypes. The lower values of heat susceptibility index (HSI) were obtained for all genotypes, in progeny PH genotypes than those observed in progeny of NH genotypes except G4 and G10 (Table 3 .(

The combined analysis of variance for all seedling and maturity traits, in progeny of heat primed and non-primed genotypes were shown in Table 4. High significant differences were obtained between control and heat stress environments for all studied traits at seedling and maturity stages except relative water content at maturity stage. Adding, highly significant differences were observed among genotypes for all studied traits. Highly and significant differences were observed between progeny of primed (P) and non-primed (N) genotypes for chlorophyll a and b contents and %TTC reduction at seedling stage and for %CMS, grain yield per plant and 1000 grain weight at maturity stage. Moreover, the shoot length, chlorophyll a content, relative water content, %CMS and 1000 grain weight showed significant differences between durum (D) and bread wheat (B) genotypes in progeny of primed and non-primed genotypes.

The variances estimated were higher in progeny of PH genotypes than observed in progeny of NH genotypes for all studied traits at seedling and maturity stages (Table 5). The PH/NH mean ratio was higher than one for all studied traits except the % germination, root length and relative water content .

The analysis of variance of four treatment combinations (NC, PC, NH and PH) for all studied traits at seedling and maturity stages are displayed in

Table 2. Progeny means of heat primed and non-primed plants for seedling traits under high and optimal temperature conditions.

	Treatment	Traits	Genotypes											
			G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	Mean	$LSD_{(0.05)}$
Progeny of non-primed plants	Control	% G.	100.0	100.0	92.86	100.0	85.71	78.57	100.0	100.0	85.71	57.14	**90.00**	**16.73**
		Sh. L	16.50	18.35	15.52	16.12	18.34	14.79	16.83	18.00	17.00	17.54	**16.90**	**2.16**
		R. L	12.07	12.51	7.45	9.13	7.90	9.33	7.71	8.79	8.75	9.88	**9.35**	**3.52**
		Chl. a	19.59	18.77	29.44	20.45	17.74	21.58	22.40	16.37	19.63	22.14	**20.81**	**3.70**
		Chl. b	11.84	10.48	14.37	12.52	10.51	13.36	13.04	9.08	10.56	11.46	**11.72**	**2.14**
		%TTC	35.03	42.02	50.35	25.01	32.55	58.40	51.26	44.98	26.35	44.38	**41.03**	**20.60**
	Heat stress	% G.	85.71	78.57	42.86	78.57	71.43	88.90	71.43	92.86	85.71	78.57	**77.46**	**22.39**
		Sh. L	13.58	14.57	14.50	12.07	10.20	10.12	14.60	10.14	16.40	12.63	**12.88**	**3.75**
		R. L	4.17	5.28	3.58	3.72	3.15	3.53	3.00	3.14	6.22	3.65	**3.94**	**1.65**
		Chl. a	4.88	5.04	8.05	9.28	3.42	3.58	8.01	5.34	7.43	7.28	**6.23**	**1.15**
		Chl. b	3.15	2.93	5.41	4.78	2.54	2.56	5.04	3.48	5.30	4.87	**4.01**	**1.92**
		%TTC	60.04	60.98	48.89	46.07	62.76	44.51	37.28	66.80	30.37	61.65	**51.94**	**16.19**
Progeny of primed plants	Control	% G.	85.71	85.71	71.43	42.86	71.43	71.43	57.14	71.43	85.71	78.57	**72.14**	**15.64**
		Sh. L	12.63	18.37	18.23	14.75	16.63	16.38	15.63	18.72	18.13	14.33	**16.38**	**3.60**
		R. L	5.38	9.73	7.98	6.22	7.38	11.38	6.75	8.23	7.63	7.50	**7.82**	**2.16**
		Chl. a	18.92	20.21	29.39	19.93	17.81	25.34	22.57	16.17	24.29	23.59	**21.82**	**2.98**
		Chl. b	10.27	11.40	14.27	11.17	9.83	14.45	13.51	8.79	12.43	11.68	**11.78**	**2.03**
		%TTC	52.90	61.60	53.78	49.54	30.05	53.22	51.27	42.64	55.16	43.98	**49.41**	**14.00**
	Heat stress	% G.	28.57	85.71	50.00	85.76	48.05	86.95	43.90	71.43	78.10	24.76	**60.32**	**30.80**
		Sh. L	7.13	17.65	8.17	13.92	11.33	13.74	14.41	16.40	17.68	10.75	**13.12**	**3.87**
		R. L	2.75	5.48	3.38	3.75	3.75	3.95	2.83	4.40	5.79	2.25	**3.83**	**1.71**
		Chl. a	5.37	6.27	8.56	7.36	4.23	3.87	9.29	6.43	11.11	7.19	**6.97**	**2.22**
		Chl. b	3.65	3.37	5.66	4.58	3.19	2.96	6.04	4.21	6.89	5.02	**4.56**	**1.39**
		%TTC	73.42	75.71	37.82	56.66	74.37	73.93	28.21	74.82	78.40	67.42	**64.08**	**14.39**

Table 3. Progeny means of heat primed and non-primed plants for maturity traits under control and heat stress conditions as well as heat susceptibility index.

	Environment	Traits	Genotypes											
			G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	Mean	$LSD_{(0.05)}$
Progeny of non-primed plants	Control	RWC	93.11	90.82	80.87	81.52	86.32	89.19	85.74	91.34	75.60	80.21	**85.47**	**2.87**
		% CMS	28.84	25.19	26.47	26.03	23.50	33.57	32.45	25.93	30.38	25.91	**27.83**	**1.66**
		1000KW	54.77	52.03	54.17	33.50	46.93	42.77	49.00	49.93	51.23	54.17	**48.85**	**3.26**
		G. yield	86.59	83.18	82.85	41.93	105.8	60.06	119.8	101.8	55.84	76.46	**81.44**	**12.0**
	Heat stress	RWC	93.01	90.51	90.06	95.06	85.91	91.25	83.47	80.96	90.95	93.36	**89.45**	**2.27**
		% CMS	55.28	34.52	38.76	47.50	45.23	43.38	28.92	45.25	58.28	21.99	**41.91**	**5.59**
		1000KW	42.37	46.93	45.47	36.33	38.53	40.03	42.40	41.73	45.50	52.37	**43.17**	**2.30**
		G. yield	16.98	27.25	39.03	25.60	28.76	29.11	36.17	31.05	29.62	39.98	**30.35**	**3.40**
		HSI	1.32	1.10	0.87	0.64	1.19	0.84	1.14	1.14	0.77	0.78		
Progeny of heat primed plants	Control	RWC	89.26	93.63	84.94	81.98	87.84	84.75	87.98	93.22	86.62	84.27	**87.45**	**1.89**
		% CMS	28.21	27.39	24.68	25.02	26.02	27.87	29.31	27.80	49.37	24.86	**29.05**	**3.65**
		1000KW	54.67	48.13	62.47	33.37	47.20	43.27	52.03	49.00	49.87	57.70	**49.77**	**3.98**
		G. yield	80.90	72.31	79.92	39.22	104.1	56.10	99.94	90.08	47.01	78.73	**74.83**	**10.8**
	Heat stress	RWC	96.74	88.64	88.17	83.24	79.52	91.24	84.10	71.47	84.16	92.08	**85.94**	**3.56**
		% CMS	66.21	47.00	46.40	43.25	42.78	55.29	22.41	43.29	81.47	32.01	**48.01**	**8.30**
		1000KW	42.60	50.83	39.23	38.93	39.43	40.53	50.93	45.70	48.47	50.57	**44.72**	**2.57**
		G. yield	21.18	37.84	48.86	21.65	40.25	31.94	35.33	38.64	32.89	23.52	**33.21**	**4.47**
		HSI	1.27	0.82	0.67	0.77	1.06	0.74	1.11	0.98	0.52	1.21		

Table 4. Means of seedling and maturity traits for NC, NH, PC and PH treatments combinations as well as variance, % CV and PH/NH Ratio.

	Mean				Variance		% CV		PH/NH
Traits	**NC**	**NH**	**PC**	**PH**	**NH**	**PH**	**NH**	**PH**	**Ratio**
Seedling traits									
% G.	90.00[a]	77.46[b]	72.14[c]	60.32[d]	197.53	582.20	18.14	40.00	0.78
Sh. L	16.90[a]	12.88[b]	16.38[a]	13.12[b]	4.93	13.77	17.23	28.29	1.02
R. L	9.35[a]	3.94[c]	7.82[b]	3.83[c]	1.07	1.31	26.22	29.85	0.97
Chl. a	20.81[b]	6.23[d]	21.82[a]	6.97[c]	4.14	5.08	32.66	32.34	1.12
Chl. b	11.72[a]	4.01[c]	11.78[a]	4.56[b]	1.39	1.76	29.38	29.12	1.14
% TTC	41.03[d]	51.94[b]	49.41[c]	64.08[a]	150.96	309.81	23.66	27.47	1.23
Maturity traits									
RWC	85.47[c]	89.45[a]	87.45[b]	85.94[c]	20.76	51.00	5.09	8.31	0.96
% CMS	27.83[c]	41.91[b]	29.05[c]	48.01[a]	125.82	276.79	26.76	34.65	1.15
1000 KW	48.85[b]	43.17[d]	49.77[a]	44.72[c]	21.20	26.52	10.67	11.52	1.04
G. Yield	81.44[a]	30.35[d]	74.83[b]	33.21[c]	46.42	80.42	22.45	27.00	1.09

NC, progeny of non-primed plants under control. NH, progeny of non-primed plants under heat stress.
PC, progeny of heat primed plants under control. PH, progeny of heat primed plants under heat stress
Values with the same letter are not significantly different according to Duncan's multiple range test at P=0.05

Table 5. Mean squares of analysis of variance among NC, NH, PC and PH treatments combinations for seedling and maturity traits.

		Seedling traits						Flowering and maturity traits			
S. O. V.	**d. f**	**% G.**	**Sh. L**	**R. L**	**Chl. a**	**Chl. b**	**% TTC**	**RWC**	**% CMS**	**1000 KW**	**G. Yield**
Rep.	**2**	17.82	0.21	0.024*	0.07	0.004	0.23	0.25	1.47	0.02	0.57
Treatments	**3**	454.61**	13.44**	22.71**	217.42**	55.94**	240.72**	9.67**	211.7**	30.42**	2174.4**
Error	**6**	9.88	0.23	0.003	0.05	0.13	2.92	0.30	2.30	0.15	3.29

*, ** Significant differences at P<0.05 and P<0.01, respectively

Table 6. Mean squares of analysis of variance for seedling and maturity traits among progeny of non-primed (N) and primed plants (P) in durum (D) and bread (B) wheat under control and heat stress conditions.

		Seedling traits					
S. O.V.	**D.F.**	**% G.**	**Sh. L**	**R. L**	**Chl. a**	**Chl. b**	**% TTC**
Tr.	**1**	4449.53**	398.37**	661.71**	6499.23**	1673.59**	4525.73**
R/Tr.	**4**	156.88*	1.21	0.02	0.69	1.48*	17.09
Geno.	**19**	1204.25**	23.47**	9.33**	38.22**	9.00**	657.97**
N vs P	**1**	9185.00**	0.65	20.36**	22.96**	2.81*	2663.42**
Among N	**9**	563.11**	9.40**	8.47**	35.99**	7.99**	607.54**
D vs B	**1**	4.07	9.63**	19.14**	15.43**	0.72	676.40**
Among D	**2**	1096.94**	4.10	18.81**	89.37**	16.54**	32.19
Among B	**6**	478.35**	11.13**	3.25**	21.63**	6.36**	787.85**
Among P	**9**	958.63**	40.08**	8.95**	42.14**	10.70**	485.57**
D vs B	**1**	67.80	28.26**	0.05	3.97**	0.11	20.76
Among D	**2**	1454.08**	100.33**	18.86**	80.75**	15.85**	784.82**
Among B	**6**	941.97**	21.96**	4.76**	23.75**	7.16**	308.86**
T x G	**19**	929.62**	11.18**	7.14**	25.23**	6.77**	828.44**
Error	**76**	57.32	1.44	0.63	0.82	0.42	30.69

		Flowering and maturity traits			
S. O.V.	**D.F.**	**RWC**	**% CMS**	**1000 KW**	**G. Yield**
En.	**1**	45.70	6286.12**	863.50**	64452.92**
R/En.	**4**	1.53	15.34	0.41	16.21
Geno.	**19**	62.12**	562.82**	161.15**	1006.66**
N vs P	**1**	17.81	63.73*	46.00**	105.68*
Among N	**9**	55.71**	329.81**	164.32**	1045.71**
D vs B	**1**	132.16**	583.76**	276.74**	0.17
Among D	**2**	90.45**	31.35	2.51	128.30**
Among B	**6**	31.40	386.97**	199.52**	1525.76**
Among P	**9**	73.45**	851.29**	170.77**	1067.73**
D vs B	**1**	321.80**	328.61**	149.21**	203.79**
Among D	**2**	65.96*	239.30**	7.50	281.27**
Among B	**6**	23.04	761.60**	152.52**	982.58**
E x G	**19**	120.21**	354.50**	60.72**	700.28**
Error	**76**	17.05	15.40	3.03	22.29

*, ** Significant differences at P<0.05 and P<0.01, respectively

Table 6. Highly significant differences among the treatment combinations were obtained for all traits.

3.3. Evaluation of stress memory for tested genotypes:

Among ten genotypes that were used in this study, the genotype G9 displayed high significant differences between progeny of PH plants and progeny of NH plants in chlorophyll a and b content, % TTC reduction and %CMS. Similarly, significant differences between progeny of PH plants and progeny of NH plants in G1 and G2 were observed for chlorophyll a and b content, % TTC reduction and %CMS. In addition, the G6 and G10 genotypes revealed significant differences between the progeny of PH plants and the progeny of NH plants in %TTC reduction and %CMS (Figure 2).

Estimated values of broad sense heritability were higher in progeny of PH genotypes than in progeny of NH genotypes for all studied traits at seedling and maturity stages, except % CMS and 1000 grain weight (Figure 3). The high broad sense heritability values were obtained in progeny of PH genotypes which amounted to 0.63 for % germination, 0.72 for shoot length, 0.55 for root length, 0.74 for chlorophyll a content, 0.81 chlorophyll b content and 0.64 for % TTC reduction at seedling stage. While, at maturity stage, the broad sense heritability values amounted to 0.75 for relative water content, 0.74 for % CMS, 0.64 for 1000 grain wheat and 0.64 for grain yield per plant. Progeny of NH genotypes given high to moderate broad sense heritability values i.e. 0.51, 0.48, 0.51, 0.63, 0.50, 0.73, 0.23, 0.81, 0.80, 0.43 for % germination, shoot length, root length, chlorophyll a content, chlorophyll b content, % TTC reduction, relative water content, % CMS, 1000 grain weight and grain yield per plant, respectively.

Denderogram constructed based on genetic distance matrix obtained from morpho-physiological traits for progeny of heat primed (P) and non-primed (N) genotypes under heat stress condition are shown in Figure 4. The denderogram grouped all genotypes into four clusters. The G9 genotype of heat primed plants (G9-P) was separated in a single branch within the dendrogram and it showed the longest genetic distance (Gd= 4.44) when compared with the G9-N (Non-primed plants). Both G10-P and G1-P genotypes were found in the next cluster and come after G9 in the genetic distance as compared with G10-N (Gd= 4.15) and G1-N (Gd= 4.00). These results were substantiated by the fact that the performance of heat primed progeny of these genotypes was significantly higher than the performance of non-primed progeny in most studied traits under heat stress. These results indicated that heat stress memory was more obvious in these genotypes. Although the G5-P and G5-N genotype showed the shortest genetic distance (Gd= 2.49), the performance of G5-P progeny was higher than G5-N progeny under heat stress as described above, indicating the existence of low level of heat stress memory in G5. The other genotypes were grouped in the last clusters and showed moderate genetic distance reflecting moderate levels of heat stress memory.

4. DISCUSSION

High temperature stress is a major constraint to the wheat productivity at all growth stages in most of the cereal growing areas especially the warmer regions of the world like the Mediterranean climate in Egypt (Fischer 1986). The epigenetic mechanisms are involved in the inheritance of tolerance to abiotic stress in trans-generational priming (Balmer *et al.* 2015). Wherefore in the present study, the effects of stress memory resulting from exposure to the high temperatures were evaluated in progeny of heat-primed genotypes. Under high-temperature stress during seedling stage, the progeny of the heat primed genotypes (PH) showed significantly higher chlorophyll a and b content and % TTC than that of the non-heat primed genotypes (NH). At maturity stage, under heat stress conditions, the grain yield per plant which is associated with the higher grain weight for progeny of PH genotypes were higher than that of NH genotypes. The greater grain weight could be resulted from the higher cell membrane thermo-stability (%CMS) and % TTC in the PH genotypes than in the NH genotypes. These results indicate to, the heat primed effect during the parents inherited for progeny which could enhance their thermo-tolerance.

Heat stress causes damage to cellular function and affects various metabolic bath-ways, especially those relating to photosynthesis, membrane thermo-stability, starch synthesis (Larkindale and Knight 2002), increase of unsaturated fatty acids and denaturation of proteins caused by high temperature disrupt ion water and organic solute movement among membranes, leading to increased cell membrane damage and in turn, cellular function inhibition **(**Cossani and Reynolds 2012). Cell membrane thermo-stability, leaf greenness, Leaf chlorophyll content and canopy temperature have been suggested as elect traits to crops improve of adaptation and yield potential of wheat under high temperature (Pradhan *et al*. 2020).

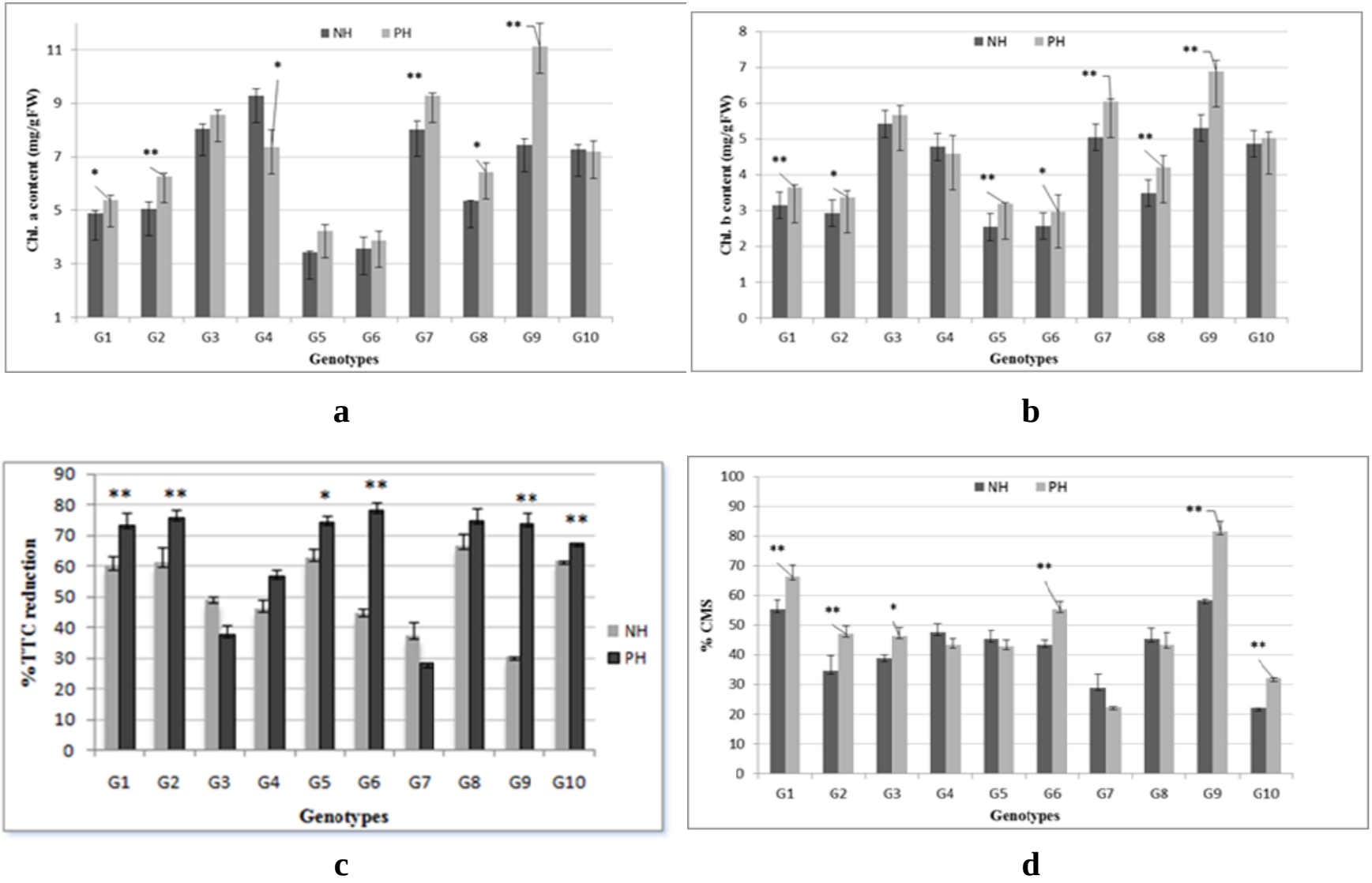

Fig. 2: Means, error bar and T-test for chlorophyll a (a) and b (b) content, %TTC reduction (c) and %CMS (d) in heat-primed (PH) and non-primed (NH) genotypes.

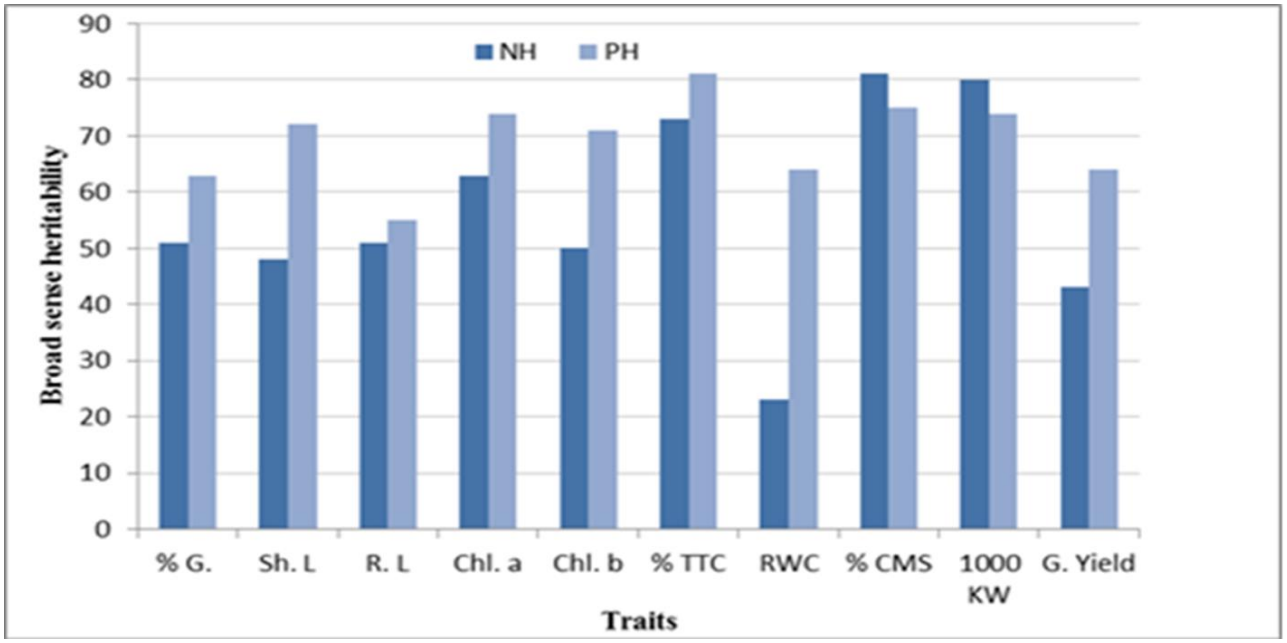

Fig. 3: The broad sense heritability for seedling and maturity traits in heat-primed (PH) and non-primed (NH) genotypes.

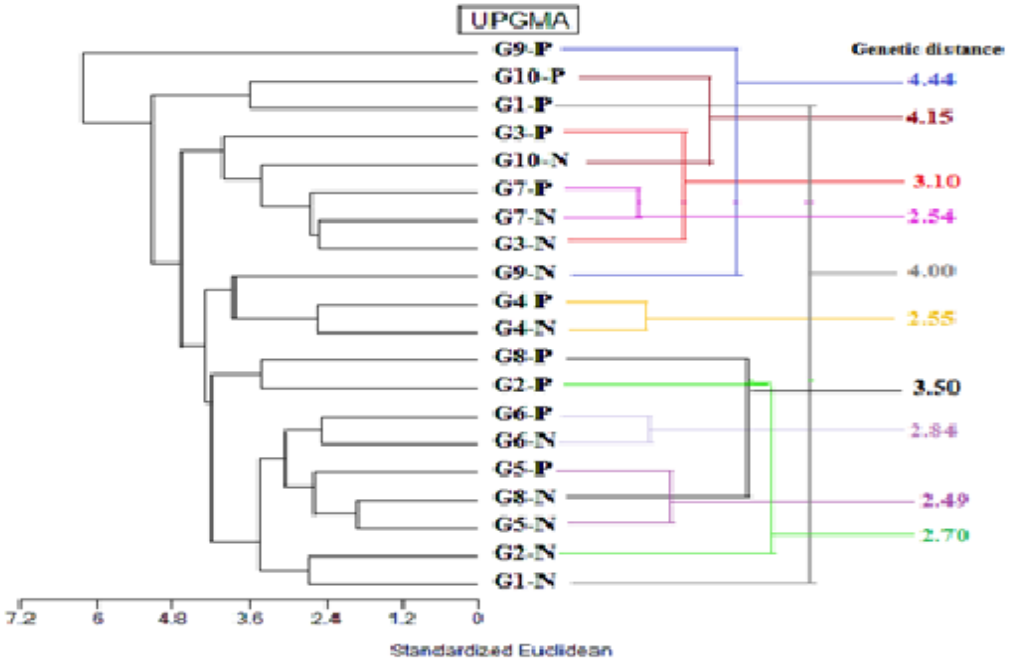

Fig. 4. Dendrogram of genetic distance using morpho-physiological data and genetic distance values between heat-primed plants and non-primed plants for each genotype.

Boyko et al. (2010) found that the progeny of heat primed Arabidopsis plants are more tolerant to many biotic stresses and that the tolerance is associated with substantially modified gene expressions, increased methylation of DNA and increased frequency of homologous recombination. Epigenetics modified like putative nucleic acid methyl transferases and binding proteins, Lysine-specific histone demethylase 1 (LSD1), RNA methyltransferase, ribosomal RNA FtsJ-like methyltransferase were expressed much higher levels in the progeny of the heat primed plants than in those of the non-heat primed plants under heat stress at

post-anthesis in wheat (Wang *et al*. 2016). The mechanisms of cell membrane thermo-tolerance to heat stress in plants have been detailed, including the heat shock proteins (HSPs), heat shock factors (HSFs), reactive oxygen species (ROS) (Driedonks *et al*. 2015). HSPs and HSFs play central roles in the thermo-tolerance of plants. HSFs are the central regulators accountable for the expression of HSP genes. 21 HSFs members are found in The Arabidopsis genome (Baniwal *et al*. 2004).

High temperature adversely affects photosynthesis in a number of ways (Shah and Paulsen 2003). Photosystem II and Thylakoid membranes are considered the most heat convertible cell components (Ristic *et al*. 2007). Thylakoid membranes under heat stress showed increased leakiness, swelling, disruption of photosystem II mediated electron transfer, and physical separation of the chlorophyll light harvesting complex II from the photosystem II core complex (Ristic *et al*. 2008). Thylakoids contain chlorophyll and damage to thylakoids caused by heat leads to chlorophyll loss (Jenner 1994).

High temperature affects morphological traits at every developmental stages in wheat, but the anthesis and pre-flowering stages are more sensitive to heat stress compared to post-flowering stages (Cossani and Reynolds 2012; Prasad *et al*. 2018). Specifically, short periods under heat stress at the flowering and pre-flowering stages can reduce yield and grain number per spike. This can be imputed to lower of pollen ability to germinate, and to the rate of growth of pollen tube (Prasad *et al*. 2018). Recently, emulations based on predictions of future environmental indicated that by year 2100 expected increases in high temperature would lead to mean grain yield reductions of 17.5 % and 7.1% for spring and winter wheat, respectively (Yang *et al*. 2017).

In the present study, the variance estimated were higher in the progeny of PH genotypes than observed in the progeny of NH genotypes for all studied traits at seedling and maturity stages, as well as, the broad sense heritability values estimated were higher in progeny of PH genotypes than in progeny of NH genotypes for all studied traits at seedling and maturity stages except % CMS and 1000 grain weight (Figure 3), indicating the effects of heat stress memory or epigenetic variations inherited in the progeny of PH genotypes. Latzel *et al*. (2013) demonstrated that epigenetic variation among inbred lines (RILs) creates diversity in phenotypes, thereby increasing the productivity and stability of plant populations. Epigenetic variation may provide additional sources of diversity within a genotypes that could be captured or created for crop improvement. It will be remarkable to understand the sources of epigenetic variation and the stability of newly formed epigenetic variants trans-generations to fully use the potential of epigenetic variation to improve crops (Springer and Schmitz 2017). Verhoeven *et al*. (2016) found that the epigenetic modifications has been well established, but still unknown, or to what degree, environmentally induced epigenetic variations are transferred trans-generations. If epigenetic signals making phenotypic diversity are inherited, they can form the basis of adaptive evolutionary change (Kronholm, and Collins 2016). Cubas *et al*. (1999) identified natural variation attributed to epialleles that affected plant traits such as floral morphology and anthocyanin content which according to Chandler (2007). Vogt (2018) explained the relationship between genetic and epigenetic variation, inheritance of the transgenerational epigenetic and the contribution of epigenetic phenotype variation and environmental adaptation in *Marbled crayfish*. High broad sense heritability was found for 1000 seeds weight in *Helianthus annuus* L. by Mostafa (2020).

In this study, G9, G1 and G2 genotypes given significant differences between progeny of PH plants and progeny of NH plants in chlorophyll a and b content, % TTC reduction, %CMS and grain yield per plant. Similarly, highly significant differences were found between progeny of PH plants and progeny of NH plants in %TTC reduction and %CMS only for G6 and G10 genotypes (Figure 2). These results indicating that the epigenetic variation is dependent on the genetic variations and it is part of the genetic variations. More than 130 epigenetic regulators were identified in Arabidopsis. Epigenetic diversity of pathways in plants is remarkable, presumably contributing to the phenotypic plasticity of plant development and the ability to survive in environments of unpredictable. Gene families encoding epigenetic modifiers can differ significantly in the number of family members between plants and mammals. (Pikaard and Scheid 2014). The prevalence of polyploidy in plants included wheat, cotton, potato, peanut, sugarcane, coffee, canola, and tobacco, suggested that it offers certain fitness advantages, such as built-in heterosis or resistance to the effects of deleterious mutations, thereby allowing duplicated genes to potentially acquire beneficial mutations, and the formation of polyploids is often associated with significant genomic and epigenetic changes (Jackson and Chen 2010). In view of the adverse effects of global climatic change, utilizing epigenetic variation for developing improved crop genotypes is of paramount importance (Singroha and

Sharma 2019). The stability and inheritance of DNA methylation among generations has been evaluated in many different ways. Perhaps the important assessment was through the analysis DNA methylation in a mutation cumulating population in *Arabidopsis thaliana* (Graaf *et al*. 2015). Thiebaut (2019) reported in some cases, the epigenetic changes can be stably inherited to the next generation. The epigenetic variations among individuals can lead to the formation of epiallels (Kalisez and Purugganan 2004). Substantial natural variation in DNA methylation patterns exists within many plant species, and this variation can influence gene expression and plant traits (Springer and Schmitz 2017).

Dendrogram constructed based on genetic distance matrix obtained from morpho-physiological traits for progeny of heat primed (P) and non-primed (N) genotypes under heat stress condition. Dendrogram divided all genotypes into four clusters. The first and second clusters contained G9-P, G1-P and G10-P genotypes of heat primed (P), which each genotype given the highest genetic distance with the same genotype of non-primed under heat stress, respectively. These results indicating that the genotypes G9, G1 and G10 may be have generated the highest stress memory or epigenetic modification inherited to their progeny. Here are more evidence indicating that epigenetic process, including heritable DNA methylation , histone modification, or chromatin re-modeling independent of DNA sequence changes (Kouzarides 2007), are closely associated to the stress memory transfer to the progeny (Boyko and Kovalchuk 2011; Iwasaki and Paszkowsk‹ 2014). The stress memory establishment is closely associated with regulation of epigenetic (Friedrich *et al*. 2019). Heat shock proteins (HSPs) play a key role in conferring heat tolerance. The principle function of HSPs is to regulate protein folding and unfolding, in conjunction with their subcellular localization and the degradation of unfolded and denatured proteins (Singh *et al*. 2016). High temperature induces the sustained accumulation of H3K4me3 and H3K9Ac on, HSP22, HSP18, HSP70 and APX2 genes. Among these genes, the accumulation of H3K9Ac andH3K4me3 in HSP22, HSP18 and APX2 but not HSP70 is HSFA2 dependent (Lamke *et al*. 2016).

In conclusion, I evaluated heat stress tolerance induced by heat primed during the parental at both flowering and grain filling stages could be passed on the progeny of parents to more effectively respond to the successive generations under heat stress during seedling stage or grain filling in wheat. This can be exemplified by less grain yield loss per plant, higher activities of dehydrogenase enzyme, better maintenance of chlorophyll a and b content and higher cell membrane thermo-stability in the progeny of heat primed plants than in the progeny of the non-primed plants. Heat stress tolerance of transgenerational was induced by heat priming in the first generation, and this might be an effective measure to cope with severe high-temperature stresses during key growth stages in wheat production.

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الملخص العربي

دراسة ذاكرة الإجهاد الحراري المتعلقة بالتحمل الحراري المكتسب في القمح

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يعتبر القمح من أهم النباتات التي تعاني بشكل متكرر من آثار الإجهاد الحراري. في هذه الدراسة، تم دراسة المعاملة الحرارية لجيل الآباء على تحمل الحرارة لنسل هذه الآباء في الأجيال المتعاقبة في مرحلتي الشتلات والنضج. أثناء مرحلة الشتلات وتحت درجات الحرارة المرتفعة ، أظهرت سلالات الأنماط الجينية المعاملة بالحرارة (PH) محتوى أعلى بشكل ملحوظ من الكلوروفيل أ و ب وزيادة في نسبة اختزال مادة TTC من ذرية الأنماط الجينية غير معاملة بالحرارة (NH). في مرحلة النضج ، تم الحصول على محصول حبوب أعلى للنبات بالنسبة للطرز الجينية المعاملة بالحرارة مقارنة بالأنماط الوراثية الغير معاملة بالحرارة تحت ظروف الإجهاد الحراري، والتي ارتبطت بشكل أساسي بارتفاع وزن الألف الحبة للأنماط الجينية المعاملة مقارنة بالأنماط الجينية الغير معاملة، كما يمكن أن ينتج الوزن الأكبر للحبوب عن الثبات الحراري العالي للغشاء الخلوي (CMS) في الأنماط الجينية المعاملة مقارنة بالأنماط الجينية الغير معاملة. كانت تقديرات المكافئ الوراثي بالمعنى الواسع أعلى في التراكيب الوراثية المعاملة مقارنة بالطرز الوراثية الغير معاملة لمعظم الصفات المدروسة في مرحلتي الشتلات والنضج. لقد اظهرت مصفوفة المسافة الوراثية التي تم الحصول عليها من الصفات المورفولوجية–الفسيولوجية، إن أعلى مسافة وراثية كانت بين النمط الجيني G9 للنباتات المعاملة بالحرارة والنمط الجيني G9 للنباتات غير المعاملة بالحرارة، والتي أعطت فروقًا معنوية جدا بين النباتات المعاملة والنباتات الغير معاملة لجميع الصفات المدروسة. مما سبق يتضح انه المعاملة الحرارية للآباء قد تؤدي إلى تحمُّل النسل للحرارة، وقد تكون هذه طريقة فعالة للتعامل مع الإجهاد الحراري الشديد أثناء بعض مراحل النمو المختلفة في القمح.