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Genetic Improvement for Grain Yield under Heat Stress Conditions in Bread Wheat (*Triticum aestivum* L.)

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Abstract

Extreme temperature is one of the abiotic stresses that causes significant yield reductions in wheat. Therefore, the current study aims to create heat-tolerant wheat plants with superior grain yield productivity by using traditional breeding. Two cycles of phenotypic directional selection for grain yield per plant were applied in two F_2 populations. These populations were derived from crosses among four local wheat varieties. In the first cycle, a directional selection for grain yield per plant was performed under both the favorable environment (optimal sowing date) and heat stress environments (late sowing date). Under the favorable conditions, the responses of F_3 plants to selection for grain yield per plant were positive and significantly higher (averaged 7.71%) than under heat stress conditions (averaged 8.20%). Moreover, the average of the concurrent response to selection for grain yield per plant in grain yield per spike had a positive and high percentage under the favorable (7.00%) and the heat stress environment (8.84%). Highly significant and positive responses were observed within the F3 plants of the two populations. The value of the average was greater under favorable (6.85%) than under the heat stress conditions (7.20%). Additionally, the 1000 kernel weight was highly significant and positive responses (5.35% and 6.11%) in both favorable and heat stress environments, respectively. Generally, the observed results indicating the F_4 plants could be a promising source to introduce yield related traits to develop high-yielding wheat cultivars for heat-stressed environments.

Keywords: Grain yield, Heat stress, Selection, *Triticum aestivum* L.

Introduction

Wheat (*Triticum aestivum* L.) is one of the three major cereal crops globally, and it is widely cultivated around the world in diverse environments (Giraldo et al., 2019). It is the leading source of plant-based protein in human food (Wu et al., 2016). In Egypt, it is the most important cereal crop with an annual production of about 9 million tons (FAO, 2021), and 775.83 million tons in the world. The climate changes, and continuously rising global temperatures significantly affects wheat production (Stone and Nicolas, 1995). Bread wheat (*Triticum aestivum* L.) is highly sensitive to high temperatures, affecting the metabolic pathways at every stage of plant development, leading to significant losses in yield (Akter and Islam, 2017). Furthermore, wheat yield is decreased by 6% for every degree Celsius increase (Lobell et al., 2008 & Asseng et al., 2015). Moreover, the anthesis and grain-filling periods are the most sensitive heat stress phases (Djanaguiraman et al., 2020). The adverse effects of high temperatures are mainly severe on grain filling, which might reduce yield by 40% (Hays et al.,2007a) and decrease, grain yield, biomass and grain number (Balla et al., 2009 and Mohammadi et al., 2011) leading to yield losses (Kumar et al., 2016). Furthermore, high-temperature exposure after anthesis declines grain filling rate and duration, which in its turn reduces grain size and weight by depressing photosynthesis, and this consequently reduces grain yield (AlKhatib and Paulsen, 1984 & Yang et al., 2002). And thus, severely reduces wheat yield and quality (Riaz et al., 2021). Additionally, heat stress restricts the life cycle and decreases plant height, spike length, and yield attributes which eventually decline grain yield (Farooq et al., 2011 and Elbasyoni, 2018). Every day, above 30°C temperature at or around flowering causes a 15%loss in yield (Telfer et al., 2013). However, the grain yield is a complex quantitative trait that is strongly influenced by interacting genetic and environmental factors. It can also down into yield components such as, spikes per plant, grain number per spike, and 1000 kernel weight (Quarrie et al., 2006 & Gao et al., 2015). Therefore, yield and yield-related traits have widely been used as heat tolerance indicators (Reynolds et al., 1994 and Pinto et al., 2010). Breeding for heat tolerance in wheat involves the identification of the genetic stocks from available gene pool, their utilization in hybridization program and the selection of breeding lines for stress tolerance using associated surrogate traits (Mishra et al., 2014). Therefore, the selection of more tolerant genotypes under the stress conditions is one of the main tasks of plant breeders and the development of heat tolerant genotypes is an issue of global concern (Clarke et al., 1992). The key to selecting stable genotypes might therefore lies in the simultaneous manipulation of genetic variability in contrasting environments at early segregating generations in a way that allows genic combinations that are superior in both situations to be incorporated into the selected genotype (Sneep, 1977 & Rasmusson, 1987). In the present study, directional phenotypic selection was performed to enhance stability of wheat genotypes for grain yield per plant in two F_2 populations under two contrasting environments (favorable and heat stress). Therefore, the main objective of the current study is to develop heat-tolerant wheat genotypes with a higher yield production.

Materials and Methods

The plant materials and field experiments:

The plant materials used in this study consisted of two segregating (F_2) populations of bread wheat (*Triticum aestivum* L.). They derived from two crosses established among four local genotypes quite variable in their performance under heat stress. The relevant information regarding the two base populations is given in **Table (1)**.

In 2019-2020 wheat growing season, a total of 100 F_2 plants of each cross were sown in the field of the Experimental Farm of the Faculty of

Table (1): Names, pedigree and origin of bread wheat genotypes used in the study.

Code	Name	Crosses established	Pedigree	Origin
1	Sakha-8		CNO67//SN64/KLRE/3/8156	Egypt
2	Sids-1	Sakha-8 × Sids-1	HD2173/PAVON"S"//1158.57/MAYA 47 "S"	Egypt
3	Gemmeiza-11	Gemmeiza-11 × Shandweel-1	B0W"S"/KVZ"S"//7C/SERI82/3/GIZA168/SAKHA61.CGM7892 -2GM—1GM-2GM-1GM0GM.	Egypt
4	Shandweel-1		SITE//MO/4/NAC/TH.AC//3*PVN/3/MIRLO/BUC. CMSS93B00567S-72Y-010M-010Y-010M- 0HTY-0SH.	Egypt

Agriculture, New Valley University in two environmental conditions, the favorable (optimal sowing date 27th November) and the heat stressed (as late sowing date 30th December) environments.

Plants were arranged in rows of 10 plants spaced 30 cm apart with plants within rows set 30 cm from each other in a randomized complete block design (RCBD) with three replications. The following characters were recorded for individual plants of each population:

Grain yield per spike (g), 1000 kernel weight (g) and Grain yield per plant (g).

The highest ten plants in grain yield per plant were selected (10% intensity) from each population in each environment, among the F_2 segregates of the two populations. To form the F3 bulk (non-selected), equal numbers of seeds from the 100 F_2 plants were pooled for each population.

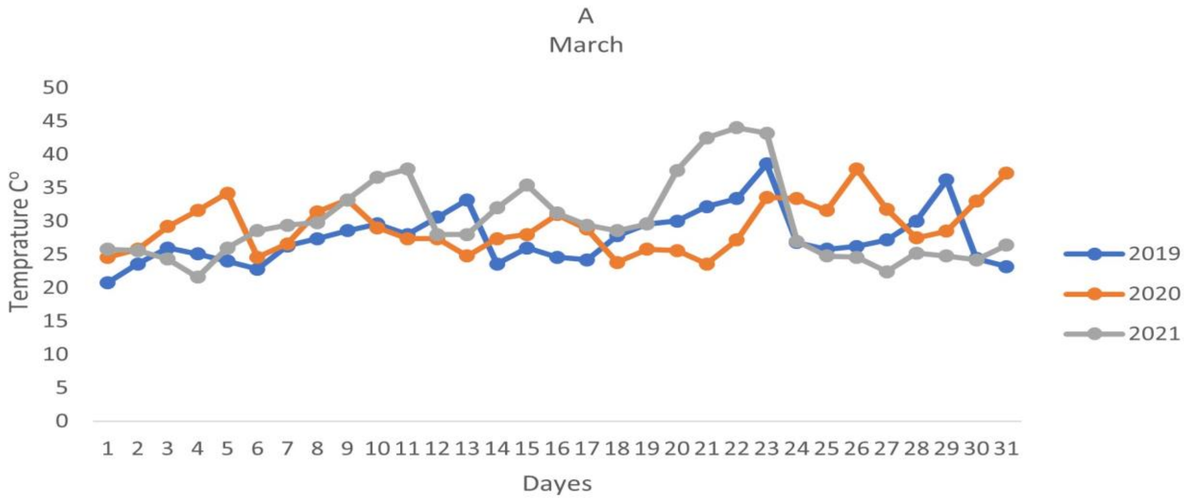
In 2020/2021 season, the 10 selected plants of each population in each environment were intermated by pair-crossing using a circular mating design without reciprocals. Which produced yielded five biparental crosses for each population. The 10 selected plants of each population in each environment along with their relevant bulks were sown in two sowing dates, the (normal sowing date 25th November) and (as late sowing date 30th December) in a randomized complete block design (RCBD) with three replications. The 10 selected plants were each represented in each block by a 10-plant row with 30x30 cm spacing's whereas 10 rows were sown for each of the five bulks.

At maturity, seeds of the 5 crosses were harvested and 30 seeds per cross were bulked in each population in each environment to form the intra population -intra environment. For each of the two F_2 populations, crosses were also made between the 10 selected plants across populations (inter-population intra-environment). The crossed seeds were harvested at maturity and 30 seeds per cross were bulked in each population to form the inter population- intra environments. Selfed seeds were also harvested separately from each individual of the 10 selected plants of each population in each environment and were kept distinct forming the F_4 selected families. From 15 random plants of each population in each environment, selfed seeds were individually harvested and kept distinct to form the F_4 non-unselected bulks. The four parental genotypes were also raised in an adjacent nursery for crossing purposes in order to obtain F_1 hybrid seeds of the two crosses.

In 2021/2022 season, seeds a total of 56 selected families were sown into the field in a favorable environment of (a normal sowing date 27th November) and heat stress (a late sowing date 30th December) environments, in a randomized complete block design (RCBD) with three replications. The 56 families tested comprised 20 F_3 selections (10 for each of the 2 populations), 30 F_3 random unselected families (15 for each of the 2 populations), 10 families of the intra-population-intra environment crosses, 10 families of the inter- population-intra environment crosses, 2 families of F_1 hybrids and 4 families of the parental genotypes. Each family along with the relevant bulk of each population in each environment and their F_1 hybrids was represented in each block by a ten –plant row with plants spaced 30 cm abort in rows set 30 cm from each other. The three main characters namely, grain yield per spike (g), grain yield per plant and 1000 kernel weight were recorded for each individual plant.

Temperature at experimental site

The maximum daily air temperatures at the experimental site **(Fig. 1A & B)** fluctuated between 20°Cand 42°C in March and between 21°C and 42°C in April in the three successive years of 2019 through 2021 (weather reports in New Valley, whttps//: W under ground.com). Several heat waves (>35°C) occurred during the post anthesis –grain filling stage of plant development in March and April each year.



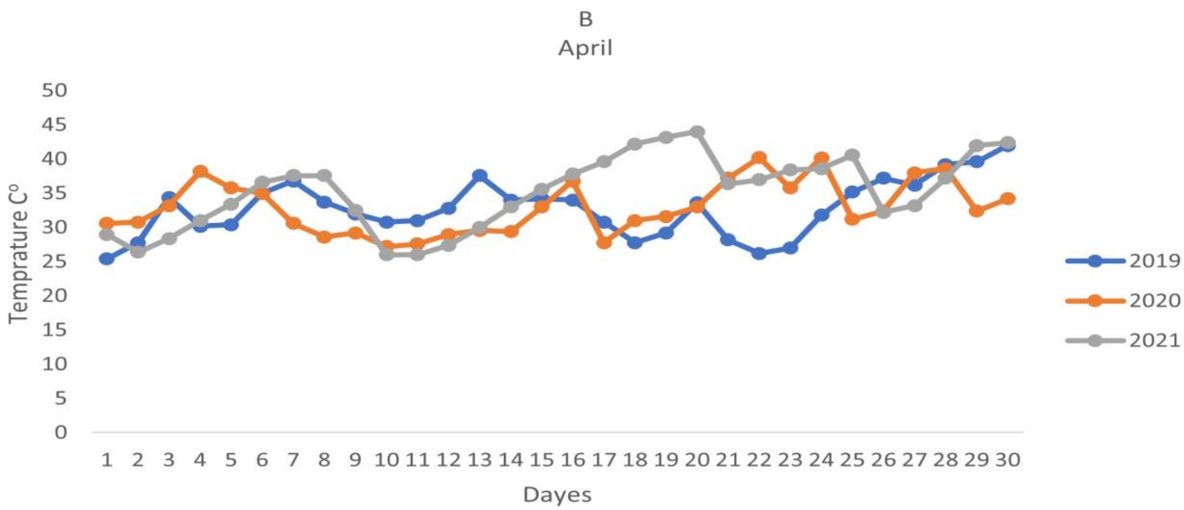


Figure (1). The recorded maximum air temperature (°C) during March (A) and April (B) of 2019, 2020 and 2021 seasons at the experimental site

Biometrical analyses

Frequency distributions of each population for grain yield per plant under favorable and heat stress environments were performed using SPSS 21.0 (SPSS Inc.). To test the significance of differences among selected plants directions as well as against the bulks of each population in each environment, phenotypic data were statistically analyzed using the analysis of variance (ANOVA) according to Gomez and Gomez (1984) was conducted.

Predicted and observed response to selection

The observed response to selection which measures the selection advance was calculated for each population in each environment as:

calculated as

$$(R\%) = \frac{Mean\ of F_3\ selcted - Mean\ of\ F_3\ bulk}{Mean\ of\ F_3\ bulk} \times 100$$

The predicted response to selection (R_x) was estimated as $R_x = i.H^2.\ \sigma P$ (Falconer, 1989). Where (i) = standardized selection differential, H^2 = heritability, and σP = phenotypic standard deviation.

Correlated response to selection

The indirect response to selection, (CR_x) was estimated as $(CR_x) = i.H^2.\ \sigma P.\ rxy$. where rxy is the genetic correlation between selected trait and unselected trait.

The % inbreeding depression was calculated as:

$$\frac{\bar{F}_1 - generation\ mean}{\bar{F}_1} \times 100$$

Genetic parameters

The following genetic parameters were estimated after Mather and Jinks (1977).

[m]: Mean of the two parents involved in the cross in each generation.

$$[m] = \frac{\bar{P}_1 + \bar{P}_2}{2}$$

[d]: The additive genetic component based on means calculated as

$$[d] = \frac{P_1 - P_2}{2}$$

[h]: The dominance genetic component calculated from means as

$$[h] = \bar{F}_1 - m$$

Genetic correlation

The genetic correlation was estimated calculated using the following formula according to Miller et al., (1958).

$$\text{Genetic correlation } (rg) = \frac{\sigma g1.2}{\sqrt{\sigma^2{}_{g\,1} \times \sigma^2{}_{g\,2}}}$$

Where: $\sigma g1.2$ the genotypic covariance between 1 and 2 traits, respectively, $\sigma^2{}_{g\,1}$ and $\sigma^2{}_{g\,2}$ are the genotypic variance of the traits 1 and 2 respectively.

The realized heritability

calculated as: $h^2 = \frac{R}{S.D} \times 100$

Where: R is the difference between the mean of selected F_3 families – mean of unselected bulk, S.D is the selection differential which is the difference between the mean of selected F_2 plants and the mean of the F_2 population.

Correlated realized heritability was estimated as, according to the following equation (Mather and Jinks,1971).

$$h^2 = \frac{\sigma^2{}_G}{\sigma^2{}_P}$$

Where: $\sigma^2{}_G$ is the genetic variance, and $\sigma^2{}_P$ is the phenotypic variance.

Parent-offspring regression (bpo) determined for each trait by regressing the means of the selected F_3 families on the values of their corresponding progenitor F_2 plants.

Results

Frequency distributions of the F_2 populations

Grain yield per plant (g)

The frequency distributions of F_2 segregates of the two F_2 populations for grain yield per plant under normal and heat stress conditions are illustrated in **(Fig. 2C- F)**.

Under the favorable and heat stress conditions the distributions displayed continuous and almost normal distributions indicating the quantitative nature of the trait and the polygenic control over it and amenable to selection in population no.1 however the distributions of population 2 under heat stress showed a skewness to the right indicating that dominance is probably operating strongly under heat stress.

Means of grain yield per plant of the selected F_2 plants in the normal and stress conditions

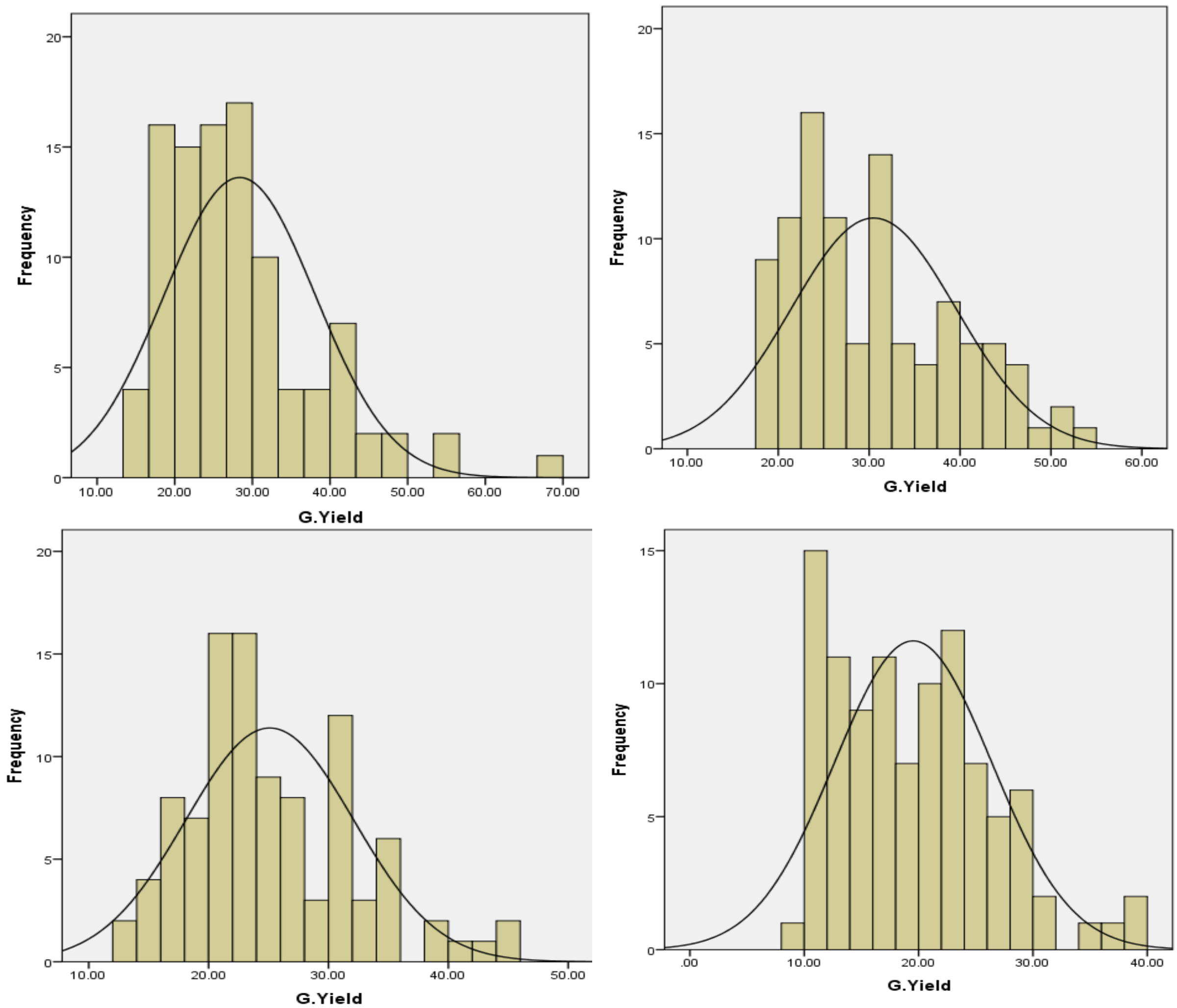


Figure (2). Distributions of grain yield per plant of the two F2 populations (C&D) under favorable and (E&F) heat stress conditions

ranged from 43.33. g to 47.14 under normal conditions in population 1, 2 respectively, with an average of 45.24g. Under stress conditions ranged from 35.84 g to 38.71 in population 1, 2 respectively, with an average of 37.10g **(Table 2).**

The selection differentials **(Table 2)** were of comparable values in the two populations under favorable conditions (ranged from 13.88 to 14.58 g) but of wider range under the heat stress (12.86 to 13.36 g). However, the averages of selection differentials over populations were almost comparable in the two environments (14.23 vs. 13.11 g).

Table (2): Means of grain yield per plant (g) under favorable and heat stress conditions of the plants selected for higher grain yield per plant with the selection differential.

Populations No	**populations Mean**		**Means of selected F_2 plants**		**Selection Differential**	
	Normal	**Stress**	**Normal**	**Stress**	**Normal**	**Stress**
1	29.45	22.62	43.33	35.48	13.88	12.86
2	32.56	25.35	47.14	38.71	14.58	13.36
Average	31.01	23.99	45.24	37.10	14.23	13.11

The impact of heat stress on grain yield per plant was quite remarkable with the unselected bulks being the most affected (an average reduction of 8.20 %) while the high selections were the least affected 7.59% **(Table 3)**.

Response to selection for grain yield per plant (g)

First cycle of selection -F_3 generation

The means of grain yield of the different generations and F_3 selections of the two populations in the favorable and heat stress environments are presented in **(Table 3)**. Highly significantly responses to conventional selection were displayed in the two populations in each of the two environments.

Under the favorable environment, the observed response for high grain yield per plant ranged from 6.43 to 8.99 % of the population means with an average of 7.71 %. Meanwhile, in the heat stress environment the observed response ranged from 7.13 to 9.27 % with an average of 8.20 %. Evidently, the observed responses were symmetrical under the two environmental conditions. Moreover, the observed responses in the two populations were greater than the low predicted responses in two environments **(Table 3)**.

Moderate to high realized heritability estimates were greater in the favorable environment (ranging from 0.46 - 0.62) than under heat stress was remarkably to high being (0.57 – 0.69). While the parent – offspring regression values measuring narrow-sense heritability were grater being 0.45 to 0.58 in the favorable environment and 0.57 to 0.66 in the heat stress environment.

Table (3): Means of the parents, bulks and F_3 families selected for grain yield per plant (g) with the observed, predicted responses (% O, P), realized heritability (h^2) and parent-offspring regressions (bpo) in the two populations under favorable and heat stress environments.

Pop. no.	Favorable environments				Heat stress environments		
	Generation	Mean (g)	%Response		Mean (g)	%Response	
			% O	% P		% O	% P
1	P_1	29.33			27.46		
	P_2	31.25			29.13		
	F_3 Bulk	35.58			32.11		
	F_3 Selected	37.87	6.43**	1.07	34.40	7.13**	0.61
	h^2		0.46			0.55	
	Bpo		0.45 ±0.29**			0.57 ±0.17*	
2	P_1	38.39			35.41		
	P_2	36.57			33.25		
	F_3 Bulk	40.25			37.65		
	F_3 Selected	43.87	8.99*	1.06	41.14	9.27**	1.85
	h^2		0.62			0.69	
	Bpo		0.58 ±0.16*			0.66 ±0.18*	
Average	F_3 Selected		7.71	1.07		8.20	1.23

*, ** Significant at P< 0.05 and P< 0.01, respectively. (% O): the observed response to selection, (%P): predicted response to selection and (Pop.no): Populations number.

Correlated responses to selection in grain yield per spike (g)

First cycle of selection – F_3 generation

The means of grain yield per spike of the different generations of the two populations in the favorable and heat stress environments are presented in **(Table 4)**. The correlated responses to selection for grain yield per plant in grain yield per spike when selection was practiced for higher grain yield per plant were positive and significant in two populations **(Table 4)**.

Highly significant and positive concurrent response obtained with selection for high grain yield per plant in grain yield per spike in the two populations under favorable environment which ranged from 6.37 to 7.63% of population mean with an average of 7.00 %. Whereas under heat stress, the correlated responses were significantly positive in two populations which ranged from 5.50 to 12.18% with an average of 8.84 % of population mean. Evidently, the correlated responses were symmetrical under both environments. The correlated responses were much greater than the very low predicted indirect responses which ranged from 0.16 to 0.26% indicating the importance of dominance **(Table 4)**.

The average grain yield per spike of the high grain yield per plant selections was greater in the favorable environment (2.50 g) than that of the unselected bulks (2.33 g) marking 7.30% increase in yielding ability. Similarly, under heat stress the grain yield per spike of the grain yield per plant selections was 2.07 g versus 1.90 g of the bulks indicating a 8.95% increase in tolerance to heat stress **(Table 4)**.

Grain yield per spike of the two populations was strongly correlated with grain yield per plant in pop.1 (r= 0.52, P<0.01), and pop.2 (r= 0.86, P<0.01), respectively under heat stress while the association was rather weaker the favorable conditions in pop.1 (r= 0.43, P<0.01), and pop.2 (r= 0.65, P<0.01). As to the heritability values estimates were generally high but higher ranging from 0.91 to 0.95 in the two populations in both environments.

Second cycle of selection- F_4 generation

Table (4): Means of grain yield per spike (g) of parents, unselected bulks and F_3 families selected together with correlated, predicted responses to selection (%CR) and realized heritability (h^2) under favorable and heat stress environments.

Pop.N0.	Favorable environment				Heat stress environment		
	Generation	Mean (g)	CR (%)		Mean (g)	CR (%)	
			% O	% P		% O	% P
1	P_1	2.01			1.72		
	P_2	2.15			1.87		
	F_3 Bulk	2.04			1.82		
	F_3 Selected	2.17	6.37**	0.16	1.92	5.50**	0.30
	h^2		0.94			0.95	
2	P_1	2.33			2.05		
	P_2	2.47			1.90		
	F_3 Bulk	2.62			1.97		
	F_3 Selected	2.82	7.63**	0.19	2.21	12.18*	0.51
	h^2		0.91			0.95	
Average	F_3 Selected		7.00	0.18		8.84	0.41

*, ** Significant at P< 0.05. and P< 0.01., respectively. (% CR): the correlated response to selection, (%P): predicted indirect response to selection and (Pop.no): Populations number.

The means of grain yield per plant values of the unselected F_3 bulks of the two populations as measured under favorable and stress environments ranged from 35.58g to 40.25g under favorable condition, with an average of 37.92g. while, under stress condition ranged from 31.36g to 37.47g with an average of 34.42g **(Table 5)**.

The ten F_3 selected plants with the highest grain yield per plant score within each of the ten families in each of the two populations displayed comparable means which ranged from 45.90g to 52.92g with an average of 49.41g under normal condition whereas under stress condition ranged from 42.76g to 47.53g with an average of 45.15g (Table 5).

The selection differentials were of comparable values in the two populations under favorable conditions (ranged from 10.32 to 12.67g) Meanwhile, under the heat stress (11.40 to 10.06 g) were of comparable magnitude in the two populations. However, the averages of selection differentials over populations were almost comparable in the two environments 11.50 vs. 10.73 g **(Table 5)**.

Table (5): Means of grain yield per plant (g) in the two F_3 populations under favorable and heat stress conditions with the means of the plants selected for higher grain yield per plant and the selection differential.

Populations No.	**F_3 mean (bulk)**		**Means of selected F_3 plants**		**Selection Differential**	
	Favorable	**Stress**	**Favorable**	**Stress**	**Favorable**	**Stress**
1	35.58	31.36	45.90	42.76	10.32	11.40
2	40.25	37.47	52.92	47.53	12.67	10.06
Average	37.92	34.42	49.41	45.15	11.50	10.73

Response to selection of the F_4 generation

Highly significant and positive responses to selection (P<0.01) for grain yield per plant (g) were obtained of the selected F_4 families, the intra environment and inter populations crosses among selections in the two populations under favorable and stress environments are given in **(Table 6)**.

In the favorable environment, the observed responses ranged from 5.34 to 8.35% of the population means with an average of 6.85%. Meanwhile, in the heat stress environment the observed response ranged from 6.97 to 7.43% of the population means with an average of 7.20 %. Evidently, the observed responses were symmetrical under the two environmental conditions. Moreover, the observed responses in the two populations were consistently greater in magnitude than those predicted responses in two environments indicating the dominance gene effects was operating **(Table 6)**.

Heat stress reduced grain yield per plant of the high F_4 selections by 6.86 %, on average, by selection within populations within environment 5.00 %, by selection with intermating between populations within environment 4.98% and by 7.14 % for the unselected bulks with an overall average reduction of generation and selections 6.00 %, relative to the non-stress environment **(Table 6).**

Selection with intermating (intra population-intra environment crossing) was generally similar to the conventional selection in the two populations in both environments. In the favorable environment, the response ranged from 9.89 to 11.71% of the population means with an average of 10.80%. Meanwhile, in the heat stress environment ranged from 12.20 to 14.48% of the population means with an average of 13.34%. The greatest responses were obtained with crossing between selections between populations in each environment (inter population -intra environment crossing). The response in the favorable environment was ranged 17.38%. while in the heat stress environment the response with ranged 20.11%. Selections with crossing of between populations across in each environment (inter population- intra environment crosses) produced plants which gave showed high grain yield per plant in both environments over all other selections, parents or F_1 hybrid **(Table 6)**.

The F_4 bulk families either initiated in favorable or stress environment displayed lower means of grain yield per plant than their corresponding F_1 in all populations and environments. Indicating considerable inbreeding depression and the importance of dominance for grain yield per plant **(Table 6).** Realized heritability estimates were generally Moderate to high ranging from 0.52 to 0.66

under favorable environment and from 0.61 to 0.74 under heat stress environment. While the parent – offspring regression values measuring narrow-sense heritability were grater being (0.47 to 0.58 in the favorable environment and 0.62 to 0.68 in the heat stress environment.

Table (6): Means of grain yield per plant (g) of parents, F_1, F_4 bulk and F_4 selected families, the intra environment and inter population crosses among selection for the two populations in the favorable and heat stress environments together with the observed, predicted responses (O, P%), realized heritability (h^2) and parent-offspring regressions (bpo).

Pop. no.	Generation	Favorable environments. Mean	%Response % O	%Response % P	Heat stress environments. Mean	%Response % O	%Response % P
1	P_1	29.43			25.51		
	P_2	31.55			29.17		
	F_1	37.68			34.58		
	F_4 Bulk	35.38			32.44		
	F_4 Selected	37.27	5.34**	2.35	34.70	6.97**	3.55
	Intra pop.intra env.	38.88	9.89**	-	36.40	12.20**	-
	h^2		0.52			0.61	
	Bpo		0.47±0.28			0.58±0.21	
2	P_1	39.23			35.61		
	P_2	37.28			33.27		
	F_1	39.74			36.87		
	F_4 Bulk	37.12			34.88		
	F_4 Selected	40.22	8.35**	3.80	37.47	7.43**	3.94
	Intra pop.intra.env.	41.47	11.71**	-	39.93	14.48**	-
	h^2		0.66			0.74	
	Bpo		0.62±0.18			0.68±0.17	
Average	F_4 Selected		6.85	5.54		7.20	5.36
	Intra pop.intra env.		10.80	-		13.34	-
	Inter pop.intra env. "F"	42.55		17.38** (% O)			
	Inter pop.intra env. "S"	40.43		20.11** (% O)			

*, ** Significant at $P< 0.05$ and $P< 0.01$, respectively. The observed response to selection (% O), predicted response to selection (%P) and Populations number (Pop.no).

The genetic parameters as estimated from generation means **(Table 7)** revealed no significant additive [d]gene effects in all populations as well as significant dominance [h] effects in two populations studied in the two environments. The sign of the dominance component [h] was uniformly positive indicating that dominance is directed towards grain yield per plant. The degree of dominance as revealed by the potence ratio [h/d] ranged from overdominance in the two populations under favorable and heat stress environments. According, inbreeding depression occurred in the F_4 bulk families of the two populations under two environments. Similarly, inbreeding depression was absence in the F4 selected families of all populations with only one exception (F_4 selections of population 1 in favorable environment), inbreeding depression but was uniformly less in magnitude than that obtained in the F4 bulk families **(Table 7)**. Inbreeding depression was generally in the absent in all populations either initiated in favorable or stress environment in the selection with intermating (intra population – intra environment). However, intermating selected plants across each environment between each population (inter population – intra environment crossing) inbreeding depression was absent in all populations under favorable and stress conditions indicating that selections were higher than their corresponding F_1 hybrid in grain yield per plant.

Table (7): Estimates of the genetic parameters [m], [d] and [h] and the % inbreeding depression of grain yield per plant (g) in two populations under favorable (F) and heat stress (S) environments.

Populations	Pop. (1)		Pop. (2)	
Parameter	Favorable	Heat stress	Favorable	Heat stress
[m]	30.49±0.78*	27.34±0.64*	38.26±0.84*	34.44±0.72*
[d]	1.06±0.78	1.83±0.64	0.98±0.84	1.17±0.72
[h]	7.19±0.82*	7.24±0.76*	1.48±0.92*	2.43±0.81*
Potence ratio [h/d]	6.78	3.96	1.51	2.07
% Inbreeding depression				
F_4 bulk	6.10	6.19	6.59	5.40
F_4 selected	1.08	-0.35	-1.21	-1.63
Intra pop. intra env.	-3.18	-5.26	-4.35	-8.30
Inter pop. intra env. "F"	-9.92			
Inter pop. intra. env. "S"	-13.15			

Correlated responses to selection in 1000 kernel weight (g).

Second cycle of selections – F4 generation

Highly significant positive concurrent responses ($P<0.01$) to conventional selection were obtained in 1000 kernel weight in the two populations in each of the two environments **(Table 8)**. The observed correlated responses in the F_4 selections initiated under favorable conditions ranged from 4.86 to 5.83% of the population mean with an average of 5.35% in the two populations under favorable environment, while under heat stress environment responses were greater ranging from 5.23 to 6.99 % of the population mean with an average of 6.11%. The observed concurrent responses were greater by far than the predicted indirect responses under both environments confirming the dominance gene effect involved in the expression of this trait **(Table 8)**.

Heat stress have had a profound effect on 1000 kernel weight was quite remarkable with the unselected bulks being the most affected (an average reduction of 6.82 %) followed by the high selection (6.14%), by within population within environment selections crosses (4.96%) while the selection with intermating across between populations were the least affected 3.66% relative to the favorable environment **(Table 8)**.

In contrast, selection with intermating produced greater correlated responses than conventional selection in the two populations in both environments. In the favorable environments, the correlated responses ranged from 8.16 to 10.12% of the population mean with an average of 9.14% but were greater under stress ranging from 11.26 to 11.46% of the population mean with an average of 11.36%. However, the correlated responses with crossing between selections across populations (inter population- intra environment crossing) was more efficient than conventional selection in producing correlated 1000 kernel weight responses among populations. In the favorable environment, the observed correlated responses ranged 14.42% but was greater under stress ranging 18.30%.

The F_4 bulk families either initiated in favorable or stress environment were lower means of 1000 kernel weight than their corresponding F_1 hybrid in all populations and environments indicating considerable inbreeding depression and the importance of dominance for 1000 kernel weight. Apparently, the means of F1 exceeded the mid-parent values under stress by 0.84 and 1.42 grams in kernel weight in populations 1 and 2 respectively, confirming that dominance controlling in 1000 kernel weight is operating **(Table 8).**

The absence of inbreeding depression in the F_4 bulk families initiated either under favorable or stress conditions indicating that selection were higher in mean grain yield per plant than their corresponding F_1 hybrid in both environments **(Table 9)**. The % inbreeding depression was manifested in the F_4 selected families of all populations either initiated in favorable or stress environments. Similarly, inbreeding depression occurred in the Selection with intermating within environment (intra population- intra environment crossing) in all populations which ranged from 5.12 to 9.24 % under the two contrasting environments. Moreover, selection with intermating between populations (inter population intra environment crosses) showed high reduced % inbreeding depression among populations in both environments. Heritability of 1000 kernel weight was quite high under favorable and stress environments which ranged from 0.91 to 0.99 in the two populations **(Table 8)**.

Table (8): Means of 1000 kernel weight (g) of parents, F_1, unselected bulks and F_4 families selected, the intra environment and the inter populations crosses among selections together with correlated, predicted responses to selection (%CR) and realized heritability (h^2) for 1000 kernel weight (g) in the two populations under favorable (F) and heat stress (S) environments.

Pop.no.		**Favorable environment**			**Heat stress environment**		
	Generation	**Mean (g)**	**% (CR)**		**Mean (g)**	**% (CR)**	
			% O	**% P**		**% O**	**% P**
1	P_1	41.34			40.92		
	P_2	43.95			41.16		
	F_1	45.50			41.88		
	F_4 Bulk	44.26			41.12		
	F_4 Selected	46.84	5.83^{**}	2.07	43.27	5.23^{**}	1.70
	Intra pop.intra env.	48.78	10.12^{**}		45.75	11.26^{**}	
	h^2		0.91			0.99	
2	P_1	45.64			43.23		
	P_2	43.17			41.45		
	F_1	46.33			43.76		
	F_4 Bulk	45.46			42.47		
	F_4 Selected	47.67	4.86^{**}	2.67	45.44	6.99^{**}	1.97
	Intra pop.intra env.	49.17	8.16^{**}		47.34	11.46^{**}	
	h^2		0.99			0.98	
Average	F_4 Selected	-	5.35		-	6.11	
	Intra pop.intra env.	-	9.14	-	-	11.36	-
	Inter pop.inra env. "F"	51.33			14.42^{**} (% O)		
	Inter pop.inra env. "S"	49.45			18.30^{**}(% O)		

*, ** Significant at $P< 0.05$ and $P< 0.01$, respectively. the observed correlated response to selection (% CR), predicted indirect response to selection (%P) and Populations number: (Pop.no).

Table (9): Estimates of the % inbreeding depression of 1000 kernel weight grain (g) in two populations under favorable (F) and heat stress (S) environments.

Populations	**Pop. (1)**		**Pop. (2)**	
Parameter	**Favorable**	**Heat stress**	**Favorable**	**Heat stress**
% Inbreeding depression				
F_4 bulk	-2.79	-1.81	-1.92	-2.95
F_4 selected	0.76	3.32	2.96	3.84
Intra pop. intra env.	5.12	9.24	6.27	8.18
Inter pop. intra env. "F"		19.87		
Inter pop. intra env. "S"		15.48		

Discussion

Tolerance to heat stress in bread wheat has been enhanced through improvement in grain yield per plant by two cycles of phenotypic directional selection under favorable and heat stress conditions using three different selection methods. The selection method used were conventional selection with selfing, selection with intermating within populations within environment and selection with intermating between population within environment.

Highly significant positive responses to selection for higher grain yield per plant obtained in the two populations were greater under heat stress in the hot environment (averaged 8.20% of population mean) than under favorable conditions (7.71% on average). Improving performance in a specific environment, selection must be conducted in that environment was studied by Jinks and Connolly (1973). This principle was also experimentally validated by Ceccarelli et al., (1998) who reported that improving grain yield in barley under stress conditions was most effectively. Apparently, selection for higher under heat stress is a form of antagonistic selection in which selection pressure acts in the opposite direction of the environment which is expected to increase the mean performance and reduce environmental sensitivity (Falconer, 1990). Evidently, the greater reductions of the F_3 families selected for higher grain yield per plant due to heat stress (7.59% on average) as compared with the unselected bulks (averaged 8.20%) indicated the F3 families selected were tolerant and less sensitive to heat stress. Similar reductions were reported by Poudel et al., (2021 a); Ahmed et al., (2022) and Singh et al., (2022) as due to heat stress of late sowing. The greater sensitivity of the selections higher grain yield per plant to heat stress conforms well with the expectations of Jinks and Connolly (1973) in that antagonistic selection which is expected to reduce environmental sensitivity.

High concurrent positive responses obtained in grain yield per spike with selection for higher grain yield per plant under heat stress were greater under high temperature (averaged 8.84%) than under favorable condition (averaged 7.00%) which lend further support to the expectations of Falconer (1990) and this can be explained as due to the correlation between grain yield per plant and grain yield per spike being much stronger under heat stress ($r= 0.86$, $P<0.01$), than under favorable conditions ($r= 0.65$, $P<0.01$). Similar results were reported by Mukherjee et al., (2008); Ramanuj et al., (2018) and Poudel et al., (2021 b) for weight of grain per spike, number of grains per spike, grain yield and 1000 kernel weight showed positive correlation and high positive direct effect on grain yield at genetic and phenotypic level respectively.

The results of the second cycle were highly significant positive responses to selection for grain yield per plant (g) were obtained in the two populations using three different methods under favorable and heat stress environments. The three selection strategies employed in this study varied in efficiency. After the second cycle, the greatest responses obtained were with intermating selections across between population within environment which resulted in genetic gains was greater (averaged 20.11 %) under heat stress condition and (averaged 17.38 %) under favorable condition. Next in efficiency was selection with intermating within populations within environments with responses was greater (averaged 13.43 %) under heat stress condition and (averaged 10.80 %) under favorable condition. The least efficient was the conventional selection with selfing with the responses being (averaged 7.20 %) under heat stress and (averaged 6.85 %) under favorable. These results are in agreement with these of Manning (1963) who reported a linear response to the first and second cycles of selection for flowering time. Moreover, second cycle of selection with intermating across populations capable producing plants for high grain yield which was greater (averaged 7.28 %) under heat stress condition and (averaged

9.54 %) under favorable condition respective high parent in two of the populations used reflecting the high efficiency of this method in bringing about a rapid selection advance. Since the same group of the selected plants of each population were intermated intra environmentally as well as inter populations. The superiority of the inter populations crosses suggests that different grain yield genes expressed under each of the two contrasting environments were incorporated into the genotypes produced by inter populations crossing. This is substantiated by the fact that the selfed progenies of the inter populations crosses where the grain yield per plant exceeded the F4 selections produced by the other two selection methods and were ranged from (averaged 6.03 to 9.54 %) for high grain yield per plant than the respective high parents of the two populations in the contrasting environments. Apparently, the directional dominance found for the genes controlling of high grain yield per plant in the two populations as well as high heritability estimates obtained for this character have contributed to the greater efficiency of that method of selection over the conventional method. This is also supported by the fact that inbreeding depression was almost absent following the inter populations environment with crossing among selection.

The remarkably high positive correlated responses in 1000 kernel weight persisted to occur under stress than under favorable conditions following the second cycle of selection for grain yield per plant obtained in the F4 families conventionally selected either with selfing which was greater (averaged 6.11%) under heat stress condition and (averaged 5.35%) under favorable condition. Meanwhile, greater positive correlated were obtained with intermating within the favorable environment which ranged (averaged 9.14 %) and (averaged 11.36 %) under stress. However, the selfed progenies of the inter population intra environment crosses displayed greater correlated responses under favorable which was greater (averaged 14.42%) than under stress conditions (averaged 18.30%) of the two populations tested. Moreover, the observed concurrent responses were greater by far than the predicted indirect responses under both environments. Since the heritability of the two traits was higher under stress than under favorable conditions. Poudel et al., (2021b) also reported similar result for high heritability were observed in grain yield and also reported similar result for high heritability were observed in grain yield and 1000 kernel weight. Evidently, the selection pressures applied by the different selection methods employed in this study might have changed the correlation between 1000 kernel weight and grain yield per plant in the two contrasting environments which could account for such changes in the correlated responses. Similar changes of correlation between 1000 kernel weight and grain yield per plant were obtained by Mukherjee et al., (2008); Riaz et al., (2010); El Ameen et al., (2013); Ramanuj et al., (2018) and Poudel et al., (2021 b) for weight of grain per spike, number of grains per spike, grain yield and 1000 kernel weight showed positive correlation and high positive direct effect on grain yield at genetic and phenotypic level respectively. Initial the F4 families selected under favorable and stress conditions for grain yield per plant of all populations exceeded their best parent in 1000 kernel weight. However, the selfed progenies of the intra population - intra environment crosses of the two populations surpassed the respective best parent in 1000 kernel weight in the favorable and stress environments. Similarly, 1000 kernel weight of the selfed progenies of the inter populations crosses exceeded the respective best parent in the two populations under the two contrasting environments. Evidently, selection with intermating either within or across populations was of efficiency in effecting correlated responded than conventional selection with selfing.

Conclusion

It can be concluded that, two successive cycles of directional selection under favorable and heat stress conditions using three different selection methods for increased grain yield under two contrasting environments. Selection with intermating within population and between populations were used for enhancing bread wheat genotypes with tolerance to heat stress conditions.

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