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RESEARCH ARTICLE

Genetic Advancement of Newly Developed Wheat Populations Under Drought-Stressed and Non-Stressed Conditions

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Abstract

Genetic variation and heritability estimates in early generations are important in identifying superior families that can be targeted for genetic advancement. Early generation selection has been a successful tool to enhance selection efficiency in plant breeding programs. The aim of this study was to select and advance F_3 families of wheat relative to their parents for drought tolerance using agronomic traits. Twelve parental lines and 66 newly-developed F_3 families were evaluated using a 6 x 13 alpha-lattice design under drought-stressed and non-stressed conditions. Considerable genetic and phenotypic variation was observed for days to heading, plant height, spike length, kernels per spike, fresh biomass, and grain yield. Expected genetic gains were high for fresh biomass and grain yield. The families LM02 x LM05, LM02 x LM23, LM09 x LM45, and LM13 x LM45 were high yielding with high biomass values and are recommended for genetic advancement using single seed descent.

Key words : Early generation selection, genotypic coefficient of variation, heritability, phenotypic coefficient of variation, wheat

Introduction

Wheat (*Triticum aestivum* L.) is a major cereal crop which is the main source of carbohydrates and protein in different regions globally. In South Africa, wheat is the most important grain crop after maize (Nhemachena and Kirsten 2017). There has been a significant decline in wheat production in the country in the last 20 years (van der Merwe 2015). Further, the national mean productivity of wheat is low at 3.76 t ha^{-1} compared with the potential yield of the crop that can reach up to 10 t ha^{-1} (Grain SA 2018). This low productivity has been attributed to various production and economic constraints including drought, heat stress, biotic stresses, and reduced profitability.

Drought stress is the greatest challenge limiting wheat productivity in the dryland production regions of South Africa. Wheat is sensitive to drought stress, and the increasing incidence of drought causes a significant reduction in both grain yield and quality. Consequently, developing drought tolerant wheat cultivars is a major goal for the [1)]Agricultural Research Council-Small Grain Institute (ARC-SGI) to improve wheat productivity in dryland growing areas of South Africa. To establish a well-characterized germplasm pool in its pre-breeding program, the ARC-SGI imported drought tolerant wheat germplasm from the [2)]International Maize and Wheat Improvement Centre (CIMMYT). A study by Mwadzingeni et al. (2016) screened drought tolerant wheat genotypes and selected lines with superior yield performance under drought-stressed and non-stressed conditions. These lines were crossed to develop a breeding population of families that were advanced to the F_2 generation (Mwadzingeni et al. 2018).

Development of new breeding populations often results in large numbers of genetic material to handle and increases the cost of drought screening. Strategies that maintain breeding

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Table 1. List of wheat parents used for half diallel analysis.

Parent	Name	Pedigree	Drought tolerance index
1	LM02	JIANG 4/4/DUCULA	0.76
2	LM04	ONIX/4/MILAN/KAUZ//PRINIA/3/BAV92	0.86
3	LM05	ACHTAR/4/MILAN/KAUZ//PRINIA/3/BAV92	0.89
4	LM09	SOKOLL*2/ROLF07	0.84
5	LM13	SOKOLL/ROLF07	0.55
6	LM17	ESDA/KKTS	0.75
7	LM21	PRL/2*PASTOR	0.82
8	LM22	MUNAL #1	0.92
9	LM23	QUAIU	1.07
10	LM29	PRL/2*PASTOR*2//SKAUZ/BAV92	0.98
11	LM45	ROLF07/YANAC//TACUPETO F2001/BRAMBLING	0.81
12	LM85	SW94.60002/4/KAUZ*2//DOVE/BUC/3/KAUZ/5/SW91-12331	0.91

progress yet reducing costs are key in running sustainable breeding programs. Early generation selection is a strategy that can be used to increase the efficiency of advancing breeding populations and reduce the cost required of screening large numbers of genotypes in succeeding generations (Abraha et al. 2017). This is achieved by fixing desirable characters and their combinations in early generations (Singh et al. 2017). Selection is done at the $F_2 - F_4$ generations to eliminate inferior lines and the most promising lines are then advanced for further analysis (Bettge et al. 2002). According to Whan et al. (1982), selection of superior families in early and late generations leads to similar yield improvement. This signifies the utility of early generation selection as a strategy that can be employed in crop improvement programs without compromising the effectiveness of selection.

Yield is a complex polygenic character which is greatly influenced by genotype by environment interaction (G x E), thus selection based on yield alone is not reliable (Ali et al. 2017). Early generation selection using agronomic- and yield-related traits can aid and improve selection for improved grain yield and drought tolerance (Fischer and Rebetzke 2018). As such, heritability estimates, genetic advances, and both phenotypic and genotypic coefficients of variability can be used to identify key traits to improve drought tolerance and enhance selection efficiency (Sohail et al. 2018). Therefore, the objective of this study was to select and advance F_3 families of wheat relative to their parents for drought tolerance using agronomic traits.

Materials and Methods

Plant materials

Twelve parental bread wheat genotypes obtained from the South African pre-breeding genetic pool were used to generate 66 hybrids, using a half diallel mating design. The parental genotypes were initially obtained from CIMMYT and were selected and advanced based on their breeding value under diverse drought-stressed and optimal conditions (Mwadzingeni et al. 2016). Table 1 provides the details of the parents used to generate the crosses and their drought tolerance index according to Mwadzingeni et al. (2016).

Field experiment

The field experiment was carried out at Ukulinga Research Farm (29° 40′ S, 30° 24′ E; 806 m above sea level) during the 2017/2018 cropping season. Test genotypes (12 parents and 66 F_3 families) were field planted using a 6 × 13 alpha lattice design, with two replications. The spacing between plants was 15 cm and the inter-row spacing was 30 cm. Five seeds were planted at each planting station and later thinned out to three plants per station. Each genotype was planted at nine planting stations giving a total number of 27 plants per treatment for each genotype. The experiments were conducted under two water regimes namely drought-stressed and non-stressed (control) conditions. Four watermark sensors (Two for drought-stress and two for the control) were used to determine the field capacity of the soil. The plants were irrigated to maintain soil near field capacity in both treatments to avoid stress in early growth stages. Drought stress was imposed on the drought-stressed treatment by withholding water to 35% of field capacity at heading, growth stage 59 according to Zadoks et al. (1974). In the non-stressed treatment, irrigation continued uninterrupted to maturity. To reduce the impact of untimely rainfall on the experiment, the soil was covered with a custom-made plastic mulch rain out system which inhibited infiltration of rain water in the experimental area.

All other standard agronomic practices in wheat production in South Africa were kept uniform on both regimes during the experiment. The weather conditions prevalent during the time of the experiment were recorded (Table 2). Weather data was recorded on day and night temperatures, precipitation, minimum and maximum relative humidity, and daily evapo-transpiration rates.

Table 2. Monthly weather data during the field trial at Ukulinga, Pietermaritzburg (2017/2018).

Year	Month	Tmax	Tmin	RHmax	RHmin	Rs	Rain	ET
2017	December	24	15	99	59	17.3	97	105
2018	January	28	16.7	99	53	20	63	126
2018	February	28	17.2	100	55	18.5	88	106
2018	March	26	16.3	100	58	16	164	98

Tmax = average maximum temperature (°C), Tmin = average minimum temperature (°C), RHmax = average maximum relative humidity (%), RHmin = average minimum relative humidity (%), Rs = average total radiation (MJ m^{-2}), Rain (mm), ET = average total evapotranspiration (mm)

Greenhouse experiment

The greenhouse experiment was carried out in a greenhouse located at the University of KwaZulu-Natal (29° 37′ S, 30° 24′ E). The greenhouse environment had day and night temperatures of 25 and 15°C, respectively. The humidity was maintained at between 45 and 55%. Plants were grown in 5 l plastic pots filled with composited pine bark growing media. The pots were arranged in a 6 × 13 alpha lattice design, with two replications. Seven plants for each genotype were grown in a single pot and thinned to five plants to ensure an even stand of plants in all pots. The experiments were carried out under two water regimes namely drought-stressed and non-stressed (control) conditions. Under both water regimes, water was applied to field capacity using a dripper system at a rate of 400 ml day^{-1} for each pot. At the heading stage of growth, irrigation was withheld in the drought-stressed treatment, but irrigation continued in the non-stressed treatment up to maturity. To avoid total crop failure in the drought- stressed treatment, irrigation was applied when the growing media had completely dried out. Control of weeds was done manually, and pests and diseases were controlled using chemicals Chess (active ingredient: pyridine azomethine) and Tilt (triazole); and a bio-control fungus *Ampelomyces quisqualis*.

Data collection

The following agronomic data were collected: 1) days to heading (DTH) were measured as the number of days until 50% of the plants had fully emerged spikes, 2) days to maturity (DTM) were measured as the number of days until 50% of the plants had reached senescence, 3) productive tiller number (TN) was measured as the number of tillers that had managed to set seed, 4) plant height (PH) was measured as the height from base of the plant to the point where the spike emerged, 5) spike length (SL) was measured from the base of the spike to the tip of the spike, 6) spikelets per spike (SPS) were measured by counting the number of spikelets per spike, 7) kernels per spike (KPS) were measured by counting the number of kernels per spike, 8) thousand kernel weight (TKW) was measured by randomly sampling 1000 kernels and weighing them, 9) fresh biomass (BI) was measured as mass of all above-ground plant parts and 10) grain yield (GY) was measured after harvesting using an electronic balance at 12.5% moisture content.

Data analysis

A combined analysis of variance (ANOVA) was performed using Genstat (18th edition) (VSN International, 2015) on data for all measured traits using the following model:

$$Y_{ijklm} = \mu + G_i + R_{j(lm)} + B_{k(jlm)} + WR_{l(m)} + S_m + G.WR_{il} + G.S_{im} + S.WR_{lm} + G.WR.S_{ilm} + \varepsilon_{ijklm}$$

where, Y_{ijklm}: observed response of genotype i in block k of replication j and water regime l of site m, μ is the grand mean, G_i is the effect of genotype i, $R_{j(lm)}$ is the effect of replication j in water regime l and site m, $B_{k(jlm)}$ is the effect of block k in replication j, water regime l and site m, $WR_{l(m)}$ is the effect of the water regime l and site m, S_m is the effect of site m, $G.WR_{il}$ is the interaction effect of genotype i and water regime l, $G.S_{im}$ is the interaction effect of genotype i and site m, $S.WR_{lm}$ is the interaction effect of water regime l in site m, $G.WR.S_{ilm}$ is the interaction effect of genotype i, water regime l and site m, ε_{ijklm} is the randomn error.

Comparisons of means was done using Fishers least significant difference at 5% level of significance. Variance components were calculated using the same program. Heritability in the broad sense was estimated using the formulae given below (Abraha et al. 2017):

$$H^2 = \sigma^2_g / \sigma^2_p$$

Where, H^2 is heritability in the broad sense
σ^2_p is the phenotypic variance for a particular trait
$= \sigma^2_p = \sigma^2_g + \sigma^2_{gs}/s + \sigma^2_e/sr$
σ^2_g is the genotypic variance for a particular trait

The phenotypic coefficient of variance (PCV) and genotypic coefficient of variance (GCV) components were computed as follows (Burton and Devane 1953):

$$PCV = (\sigma_p/\bar{X}) \times 100$$
$$GCV = (\sigma_g/\bar{X}) \times 100$$

Where:
σ_p is phenotypic standard deviation
σ_g is the genotypic standard deviation
$\bar{X}$ is the mean performance for a particular trait
Genetic advance (GA) and the genetic advance as percent of mean (GAM) were calculated using the following formulae

Table 3. Mean squares and significant tests from combined analysis of variance involving ten phenotypic traits of 78 wheat genotypes evaluated in two sites, under two water regimes and two replications.

Source of variation	df	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	BI	GY
Block	40	13.44***	22.24*	23.87	1.34	128.14**	25.66	20.22	4.61	21361.00	6566.00
Replication	4	3.39	5.963	8.12	24.05***	575.33***	5.18	1.37	41.42	664793.00***	189193.00***
Genotype	77	25.18***	19.69***	45.11***	1.13*	151.52***	21.65	32.39***	27.99**	34020.00	8991.00
Site	1	73.39***	9424.08***	145.39**	2043.78***	15051.71***	1244.17***	4250.21***	736.66***	30683941.00***	4101033.00***
Water Regime (WR)	2	176.64***	3091.86***	261.05***	135.80***	672.65***	69.73	1674.48***	17107.67***	14272314.00***	4520338.00***
Genotype x Site	77	3.05	9.74	22.42*	1.02	34.07	21.12	14.97	22.50	27092.00	7587.00
Genotype x WR	77	1.99	5.83	18.14	0.76	33.72	20.64	13.98	14.81	29268.00	8742.00
Site x WR	1	29.64***	346.51***	5.21	6.26**	4.02	116.46	545.46***	5548.27***	6977520.00***	2237842.00***
Genotype x Site x WR	77	2.06	8.84	20.30	0.93	29.21	23.36	14.01	18.41	24923.00	7145.00
Residual	111	2.33	7.49	15.71	0.84	32.02	22.70	15.77	17.32	26462.00	8126.00
Total	467	5.70	30.643	21.68	4.45	73.71	24.39	28.04	56.83	111848.00	25791.00

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield

(Johnson et al. 1955):

$$GA = k\ H^2\ \sigma_p$$

Where:

GA = Genetic advance

k is the coefficient of selection intensity

H^2 is heritability in the broad sense for that specific trait

σ_p is the phenotypic standard deviation of that specific trait

Finally, genetic advance as percentage of mean (GAM) was computed as follows (Abraha et al. 2017):

$$GAM = (GA / \bar{x}) \times 100$$

Results

Analysis of variance

A combined analysis of variance showing degrees of freedom, mean square values, and significant tests is presented in Table 3. Highly significant differences ($P < 0.01$) were observed among genotypes for DTH, DTM, PH, SL, KPS, and TKW. Significant differences were also observed for TN ($P < 0.05$). The mean squares for site and water regime were highly significant ($P < 0.01$) for all traits except for SPS for water regime. Significant genotype by site interaction ($P < 0.01$) was observed for PH only. There was no genotype x water regime interaction for all the studied traits. The interaction of water regime and site was significant for most traits except PH, SL, and SPS.

Yield and agronomic performance

The overall mean grain yield observed for the genotypes was 143.62 g m^{-2} and 317.22 g m^{-2} under drought-stressed and non-stressed conditions, respectively (Table 4). Yield reduction of 54.73% was observed because of drought stress. The highest yielding families under stress were LM02 x LM05, LM13 x LM45, LM02 x LM23, and LM09 x LM45 with mean yields of 199.80 g m^{-2}, 185.20 g m^{-2}, 179.30 g m^{-2} and 175.60 g m^{-2}, respectively. As expected, performance of genotypes was better in non-stressed conditions than in stressed conditions for DTM, PH, TN, SL, SPS, KPS, TKW, BI, and GY (Table 4). The DTH were similar in both drought-stressed and non-stressed conditions. The DTM reduced by 4.45 days due to the effect of drought stress. The least DTM were observed for crosses LM17 x LM85, LM45 x LM85, LM17 X LM29, LM04 X LM45, and LM09 x LM21. Drought stress reduced the average PH, TN, SL, SPS, and KPS. Decreased TKW and BI were recorded with 26.84 and 43.12%, in that order, due to the effects of drought stress.

Variance components

GCV, PCV, H^2, GA, and GAM are presented in Tables 5 and 6. PCV values were higher than GCV values for all the traits and both water regimes. Under non-stressed conditions, the highest GCV values were observed for GY (8.11%), BI (7.26%), and KPS (6.93%). The highest GCV values in drought-stressed conditions were for TN (6.56%), GY (6.43%), and KPS (5.43%).

Heritability estimates

The heritability among the traits varied in both drought-stressed and non-stressed conditions (Tables 5 and 6). Heritability estimates were generally higher in non-stressed condition than drought-stressed conditions for all traits except fresh biomass and grain yield. High heritability was observed in stressed conditions for BI (93.53%) and DTH (78.81%). Under non-stressed conditions only DTH showed high heritability (84.11%). Spike length with values of 67.31% and 60.98% had moderate heritability under both water regimes.

Table 4. Mean values of the ten best genotypes and five bottom genotypes (based on grain yield g m^{-2}) for ten quantitative traits of 12 parents and their 66 F_3 families.

Entry	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
top ten genotypes																				
LM02 x LM05	50.00	49.75	86.00	80.75	66.17	62.82	4.08	3.63	73.10	67.68	13.11	12.69	34.02	25.12	40.06	30.12	799.70	469.80	395.00	199.80
LM13 x LM45	49.00	50.00	85.50	81.00	65.37	65.10	5.10	3.85	85.00	81.78	14.86	13.60	25.22	21.70	43.13	30.73	863.10	468.90	420.00	185.20
LM02 x LM23	51.00	51.25	85.75	81.50	68.35	65.65	5.13	3.50	82.75	73.95	13.77	11.93	25.35	23.09	45.08	30.55	832.50	463.20	458.00	179.30
LM09 x LM45	49.00	50.75	84.00	81.50	62.60	63.05	4.13	3.73	72.00	69.99	13.21	12.70	22.38	22.21	39.97	31.99	561.30	439.30	237.00	175.60
LM13	51.25	52.50	85.00	82.75	62.60	66.00	4.35	4.08	70.70	75.75	13.37	14.20	26.10	25.59	36.48	26.21	736.30	463.30	350.30	175.50
LM13 x LM85	47.75	50.50	84.00	81.00	63.82	61.97	4.65	4.15	69.60	71.53	12.96	13.64	24.94	22.66	40.02	29.44	712.20	481.30	324.10	173.20
LM02 x LM21	48.00	49.00	85.75	80.50	56.90	59.65	3.50	3.58	67.60	74.80	11.20	12.70	23.15	24.48	37.48	31.45	525.60	422.70	229.00	172.90
LM04 x LM21	49.50	49.25	84.75	80.75	58.12	60.90	3.95	3.73	78.10	74.99	14.45	13.50	27.72	19.26	41.01	38.49	637.40	425.30	304.60	169.30
LM22 x LM23	47.25	50.25	85.50	81.75	64.62	64.60	4.08	3.53	75.00	71.27	13.61	13.00	28.66	24.44	39.40	30.09	750.40	436.50	313.80	167.70
LM02 x LM17	49.00	49.50	86.00	80.50	62.37	65.05	4.65	3.98	72.85	69.75	12.26	12.64	23.80	27.38	39.41	29.30	635.30	406.00	287.20	166.80
bottom five genotypes																				
LM05 x LM85	48.50	49.75	84.25	79.75	60.42	60.45	4.18	3.00	68.55	65.04	41.12	12.60	23.61	21.01	39.22	26.55	589.30	333.80	244.60	113.80
LM85	51.75	51.25	85.25	78.25	61.02	62.45	4.30	2.80	73.55	72.14	13.87	13.25	26.44	23.55	37.55	23.80	660.20	382.00	295.40	113.00
LM17 x LM85	46.75	48.00	82.00	76.50	61.67	58.20	4.83	3.63	73.70	69.57	12.35	12.04	23.64	21.40	40.18	23.82	750.30	312.70	382.90	110.60
LM05 x LM17	48.75	50.00	84.00	80.50	64.02	55.72	3.95	3.14	73.60	70.44	13.23	12.25	26.90	20.15	37.85	30.54	631.00	379.10	284.00	101.10
LM05 x LM22	56.00	57.25	92.00	84.50	66.02	59.47	5.20	2.50	72.55	67.41	14.06	13.09	27.21	18.21	36.85	29.54	1088.40	342.30	460.00	90.00
Mean	49.56	50.63	84.92	80.47	62.38	61.09	4.51	3.57	74.00	71.88	13.54	12.83	25.21	22.22	39.31	28.76	701.47	399.00	317.22	143.62
CV (%)	2.52	3.01	3.27	2.88	6.58	5.73	21.81	22.90	7.53	7.19	48.42	8.41	16.53	16.54	8.59	14.34	29.11	20.10	35.89	25.18
SED	0.88	1.08	1.96	1.64	2.90	2.48	0.70	0.58	3.94	3.65	4.63	0.76	2.96	2.58	2.38	2.92	144.40	56.72	80.13	25.62
LSD (5%)	1.75	2.13	3.88	3.24	5.74	4.90	13.75	1.15	7.79	7.23	9.16	1.51	5.85	5.11	4.72	5.77	285.60	112.20	158.50	50.68

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = productive tiller number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g m^{-2}), GY = grain yield (g m^{-2}), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Low heritability ($H^2 < 50\%$) was observed for DTM, PH, TN, SL, SPS, KPS, TKW, and GY under both water regimes. The heritability of GY were 17.64% and 14.42%, KPS were 28.47% and 41.28%, and PH were 32.62% and 34.46% under drought-stressed and non-stressed conditions, in that order. BI had low heritability value of 17.59% in non-stressed conditions.

Genetic advance

The expected genetic advance varied widely under drought-stressed and non-stressed conditions for the measured traits (Tables 5 and 6). Higher genetic advances of 29.73 and 6.84% were recorded for BI and GY under drought stressed conditions, respectively. However, the genetic advances of the two traits were 37.61 and 17.12% under non-stressed conditions, in that order. Other traits including DTH, DTM, PH, TN, SPS, KPS, and TKW showed relatively low values of expected genetic advance varying from 0% for TN to 2.56% for DTH under bother water regimes except spike length which had a genetic advance of 5.01 and 6.09% under drought-stressed and non-stressed conditions, respectively. The GAM was the highest for BI (7.45%), SI (6.97%), and KPS (5.10%) under drought-stressed condition. The GAM for spike length was 8.23%, kernels per spike (7.84%), days to heading (5.65%) and GY (5.42%) under non-stressed conditions. All the other traits such as DTM, PH, SPS, and TKW show moderate to low GAM.

Discussion

The high significant values of genotypes for DTH, DTM, PH, TN, SL, KPS, TKW, and BI (Table 3) indicate that the tested families show abundant genetic variation for effective selection for drought tolerance using agronomic traits. Similar results of high genotype differences for these traits have been reported in different moisture regimes in wheat (Eid 2009; Mwadzingeni et al. 2017). The non-significance of genotypes by site by water regime interaction for all the traits indicated that the environments were not highly discriminative of the test genotypes. Increasing the number of test environments may provide a better inference and improve our understanding on the G x E effects of the selected genotypes.

The significant differences observed among genotypes when tested under drought-stress conditions except for spikelets per spike indicate the negative influence of moisture stress on the expression of the assessed traits (Table 4). This led to

Table 5. Genetic parameters for morphological characters and yield components in 78 wheat genotypes under drought stressed conditions.

Trait	GCV (%)	PCV (%)	H^2 (%)	GA (%)	GAM (%)
DTH	3.23	3.64	78.81	2.56	5.05
DTM	0.96	2.13	20.17	0.61	0.76
PH	2.56	4.48	32.62	1.57	2.57
TN	6.56	14.21	21.32	0.19	5.33
SL	5.07	6.49	60.98	5.01	6.97
SPS	2.22	4.96	19.96	0.22	1.74
KPS	5.43	10.18	28.47	1.13	5.10
TKW	0.00	8.74	0.00	0.00	0.00
BI	4.38	4.53	93.53	29.73	7.45
GY	6.43	15.31	17.64	6.84	4.75

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length , SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield, GCV = genetic coefficient of variation, PCV = phenotypic coefficient of variation, H2 = Heritability, GA = genetic advance, GAM = genetic advance as a percentage of the mean

Table 6. Genetic parameters for morphological characters and yield components in 78 wheat genotypes under non-stressed conditions.

Trait	GCV (%)	PCV (%)	H^2 (%)	GA (%)	GAM (%)
DTH	3.50	3.82	84.11	2.80	5.65
DTM	1.25	2.31	29.44	1.02	1.20
PH	2.76	4.70	34.46	1.78	2.85
TN	0.00	12.66	0.00	0.00	0.00
SL	5.70	6.95	67.31	6.09	8.23
SPS	0.00	24.46	0.00	0.00	0.00
KPS	6.93	10.79	41.28	1.98	7.84
TKW	3.73	6.27	35.27	1.53	3.89
BI	7.26	17.32	17.59	37.61	5.36
GY	8.11	21.36	14.42	17.12	5.42

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield, GCV = genetic coefficient of variation, PCV = phenotypic coefficient of variation, H2 = Heritability, GA = genetic advance, GA = genetic advance as a percentage of the mean

reduced performance of genotypes for these traits due to impaired physiological performance as pinpointed by Farooq et al. (2014) who stated that drought affects wheat physiology by reducing metabolic functions, reducing stomatal conductance, causing tissue dehydration and increasing leaf senescence. Reduced performance due to drought stress in yield components has also been reported in other studies (Allahverdiyev et al. 2015; Saleem 2003). The genotype by water regime interaction was non-significant for all traits indicating that the genotypes kept their rankings in the different water regimes.

The presence of high CV (Table 4) for some traits such as GY and BI was expected and thus selection based on yield alone is not dependable. The high CVs also show the variability that is associated with drought trials making them harder to repeat than other agronomic trials (Rehman et al. 2015). Low CVs were recorded for DTH, PH, and SL showing that these traits could be used with more reliability for evaluating genotypes.

Higher PCV values than the GCV values (Tables 5 and 6) were observed for the tested traits indicating the effect of the environment on the phenotypic expression of the traits (Ali et al. 2008). However, the GCV and PCV values of DTH and BI (Table 5) were almost equal under drought-stressed conditions indicating that most of the variation for these traits would be attributable to genetic effect (Khan and Naqvi 2011). This provides a great opportunity for efficient selection using these traits because their expression is controlled to a large degree by the genetic variation of the genotypes. DTH is an important trait for selection for drought tolerance. This trait is a means of drought escape ensuring higher yields under terminal drought stress. This provides a great opportunity for selection for early heading and maturing genotypes with high yield potential under drought-stressed condition (Abraha et al. 2017).

High heritability for a trait shows that the phenotypic expression of the genotype is a good indicator of the genetic potential of the genotype. BI showed low heritability under non-stressed conditions but showed high heritability under drought-stressed condition (Tables 5 and 6). Similar results have been reported by Ahmadizadeh et al. (2011). Low her-

itability observed for DTM, PH, KPS, and TKW under both stressed and non-stressed conditions (Tables 5 and 6) indicate a large impact of the water regime and the sites on the expression of these traits. The heritability for these traits was much lower in the drought-stressed conditions than non-stressed conditions suggesting the impact of drought-stress on reducing heritability of key traits. The decrease in heritability values under drought-stressed condition signifies the difficulty in selection of genotypes for drought tolerance under stress necessitating testing of genotypes in both well-watered and drought-stressed conditions. Similar result showing reduced heritability values under drought stress were reported by (Dorostkar et al. 2015; Eid 2009; Shukla et al. 2015). Therefore, based on the observed heritability, selection using DTM, PH, TN, KPS, and TKW may not lead to any genetic gain being realised.

High heritability alone is not sufficient in predicting the breeding value of a genotype but only informs of the amount of genetic variation that is expressed in the phenotype. Genetic advance serves to estimate the expected response to selection for a certain trait. Therefore, occurrence of high heritability and high genetic advance signify the presence of additive gene action for the trait and thus selection for that trait will lead to genetic gain for that trait (Jatoi et al. 2012). Under such conditions, employing early generation selection is advisable as selection at this stage will be effective in identifying superior families. High heritability was recorded for DTH under both water regimes with high levels of genetic advance (Tables 5 and 6). The similarities in both water regimes was expected as drought stress was imposed at heading stage and therefore there was no impact of stress on this trait. DTH and DTM can be exploited to produce early maturing genotypes that escape drought stress by initiating the reproductive phases of growth when the impact of terminal drought has not set in. The genotypes that showed the least number of days to heading and could be selected for drought escape are LM04 x LM45, LM17 x LM85, LM17 x LM23, LM22 x LM85, LM17 x LM22, and LM09 x LM17.

Fresh biomass showed the highest genetic advance under both drought-stressed and non-stressed conditions showing great potential for early generation selection. However, only in the stressed environment was the highest genetic advance observed in the presence of high heritability. This suggests that the genetic component for fresh biomass is greatly expressed when the plants experience terminal drought stress. Therefore, selection for increased fresh biomass at early generations can lead to substantial genetic gains if selected for in stressed conditions. High biomass in wheat is associated with greater stem and leaf area. This leads to higher yields as the plant has increased photosynthetic area which increases photo-assimilate accumulation (Taheri et al. 2011). This is in agreement with Blum (2009) who suggested that enhanced biomass production due to effective use of water is the major contribution to improved genotypic performance under drought stress. All the top ten genotypes (Table 4) in this trial showed higher than mean values for BI under drought-stress. This is ideal for drought tolerance improvement as reported by del Pozo et al. (2016), who state that the annual increases in wheat yield that have been achieved since the 1960s have been positively correlated to above ground biomass.

Longer SL is a desired trait under stress as it is associated with higher grain number (Ahmed et al. 2016). Moderate heritability observed for spike length in both water regimes (Tables 5 and 6) was accompanied with high genetic advance. Therefore, selection for improved spike length at this stage will not be effective. Therefore, selection will need to be delayed until later generation for it to be effective (Rehman et al. 2015).

Grain yield showed high genetic advance, but the heritability was low in both water regimes. This low heritability for grain yield suggests that the genetic makeup of the genotypes can be influenced under drought-stressed condition. This is further supported by Ahmad et al. (2017) who reported that a low response to selection coupled with low heritability could be a result of environmental error and not a lack of genetic variation. This explains the influence of the environment on GY and the need to use component traits for indirect selection. The highest yielding families in drought stressed conditions were LM02 x LM05 (199.8 g m^{-2}), LM13 x LM45 (185.2 g m^{-2}), LM02 x LM23 (179.3 g m^{-2}), and LM09 x LM45 (175.6 g m^{-2}). The top three genotypes performed relatively well in both drought-stressed and non-stressed conditions. This agrees with the findings by Foulkes et al. (2007) and Mwadzingeni et al. (2016) who reported that genotypes that had high yield potential under optimum moisture conditions also performed well under drought stress. Therefore, early generation selection could be effective as the higher yields obtained in the top genotypes is accompanied by higher than the mean performance for TKW and BI. Higher yielding families should be advanced to the F_4 generation using single seed descent.

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