Research

Agronomic performance and water use efficiency of newly developed wheat populations under drought-stressed and non-stressed conditions

Maltase Mutanda[1,2] · Hussein Shimelis[2] · Vincent Chaplot[2,3] · Kwame W. Shamuyarira[4] · Sandiswa Figlan[1]

Received: 29 July 2024 / Accepted: 7 February 2025
Published online: 25 February 2025

Abstract

Limited and variable rainfall conditions during flowering and grain filling stages remain the leading cause of poor yields and quality in the major produced crops, including wheat. Cultivating water-use-effici t wheat cultivars will buffer yield stability and environmental plasticity to achieve food security and economic opportunities. Therefore, this study aimed to evaluate the agronomic performance and water use efficie y (WUE) of newly bred wheat populations under drought-stressed and non-stressed conditions to select drought-tolerant families for genetic advancement and production. Field experiments were conducted in the 2022 and 2023 growing seasons to evaluate 100 genotypes (10 parental lines and 90 families) using a 5 × 20 alpha-lattice design under drought-stressed (DS) and non-stressed (NS) conditions. Controlled experiments were conducted using custom-made plastic mulch under field conditions. The following agronomic traits were recorded: number of days to 50% heading (DTH), number of days to 50% maturity (DTM), plant height (PH), number of productive tillers (TN) per plant, spike length (SL), number of spikelets per spike (SPS), spike weight (SW), grain yield (GY), shoot biomass (SB), root biomass (RB), and total plant biomass (PB). The water use efficie y for grain yield (WUE_{gy}), shoot biomass (WUE_{sb}), root biomass (WUE_{rb}) and total plant biomass (WUE_{pb}) were calculated. Eight drought tolerance indices were computed based on grain yield response under DS and NS conditions. Significa t ($p < 0.05$) genetic variations were recorded for agronomic traits and WUE variables. The mean grain yield value of the F_3 families was higher by 29.42% and WUE by 25.00% than the parental lines under DS conditions. Among the F_3 wheat populations, the WUE_{gy} ranged from 0.05 g mm^{-1} (LM47 X LM70) to 0.21 g mm^{-1} (BW141 X LM71) under DS conditions, whilst the WUEgy for the parental lines ranged from 0.08 (BW162) to 0.18 (LM48) under DS. Twenty one percent of the wheat populations had greater drought indices than parental lines. Families, BW141 X LM71, LM71 X BW162, BW140 X LM70, BW162 X BW140, BW141 X LM26, BW162 X LM71, BW152 X LM71, LM70 X BW141, LM75 X LM47 and LM70 X BW140 were selected for their high grain yield production and high WUE_{gy} under DS conditions. These genotypes are recommended for further selection and deployment as new cultivars in South Africa or other water-limited agro-ecologies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42452-025-06605-1.

✉ Maltase Mutanda, 19283849@mylife.unisa.ac.za | [1]Department of Agriculture and Animal Health, University of South Africa, Florida 1709, South Africa. [2]School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Scottsville, Private Bag X01, Pietermaritzburg 3209, South Africa. [3]Laboratory of Oceanography and Climate, Experiments and Numerical Approaches (LOCEAN), UMR 7159, IRD/C NRS/UPMC/MNHN, IPSL, Institut de Recherche Pour le Dévelopement (IRD), 75005 Paris, France. [4]Department of Plant Sciences, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa.

Highlights

- Drought stress significa tly reduce grain yield production of wheat genotypes.
- The water use efficie y potential of wheat genotypes is negatively affected by drought-stressed conditions
- Utilization of drought indices enables the effici t selection of high-grain yield genotypes under drought stress.

Keywords Biomass production · Drought stress · Grain yield · Mean productivity · Water use efficie y

1 Introduction

Wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is globally the second most widely produced cereal crop after maize [1]. It supplies about 20% of the calories [2] and up to 60% of proteins in human nutrition [3]. The rapid increase in global population and the adverse effects of climate change are expected to increase wheat demand to between 35 and 56% by 2050 [4]. Out of 220 million hectares of world agricultural land cultivated by wheat, only 10 million hectares (4.55%) are cultivated in Africa to produce about 25 million tonnes of grain per annum [5]. Further, the wheat production in sub-Saharan Africa (SSA) is 7.5 million tonnes per annum, far less than the estimated demand of approximately 31.1 million tonnes for human consumption. To meet regional demand, SSA imports approximately 26.6 million tonnes of wheat annually [6, 7].

Climate change is predicted to exacerbate the frequency and severity of drought stress, making it more challenging to improve wheat production [8]. Enhancing wheat production under climate-induced drought episodes will be challenging, considering that 66% of global wheat production is under dryland conditions [9]. Since the green revolution, rapid irrigation developments have been made to reduce the impact of drought stress on crop production, but this has led to increased water demand, making agriculture the largest dependent on freshwater globally [10]. Selecting water-use effici t and drought-adapted wheat cultivars emerges as a promising solution to reduce the water demand and enhance crop resilience to drought. This will enable water conservation for multiple utilities and maintain sustainable food systems.

Screening genetically diverse populations is vital in wheat breeding and for the selection of drought-tolerant and water-use effici t wheat genotypes. Water use efficie y (WUE) is an important indicator that exhibits genotypes' ability to produce grain yield under limited irrigation regimes and soil moisture levels [11]. The WUE of plants is decreased under a water defici , but plants that can maintain their physiology and reduce their water use have a specific drought adaptation mechanism [12]. The decrease in WUE is due to a higher transpiration rate and reduced carbon assimilation under drought stress [13], and some of the test genotypes could fail to produce optimum yield. Hu et al. [14] asserted a decrease in WUE and GY under drought stress in wheat. Whilst, Alotaibi et al. [15] and Zhang et al. [16] reported an increased WUE in wheat under limited water regimes. Nevertheless, Yong'an et al. [17] and Boutraa et al. [18] found a significant decrease in wheat WUE under drought-stressed conditions. Given the variations in WUE under drought stress, as highlighted above, a comprehensive understanding of the impact of drought stress on WUE of newly bred wheat varieties provides a foundation for breeding aimed at developing wheat genotypes with enhanced drought tolerance and improved WUE.

Several studies have suggested the breeding of water-use effici t wheat varieties as a promising strategy to improve wheat production [15, 17], but there are still very few varieties with stable water-use efficie y and drought tolerance expressed under different environmental conditions. To harness the genetic variation of wheat for drought adaptation and water use efficie y under South African conditions, a wheat breeding group at the University of KwaZulu-Natal's African Centre for Crop Improvement sourced 100 wheat lines from the International Maize and Wheat Improvement Centre (CIMMYT) heat and drought nursery [19]. The genotypes were phenotyped for plant biomass production under limited irrigation conditions in Pietermaritzburg, South Africa. Eight out of the 100 wheat lines from CIMMYT were selected based on high biomass production, and two drought-tolerant South African wheat lines were crossed to generate new wheat families, which were advanced to F_2 families by Shamuyarira et al. [20]. The parental lines and their F_2 wheat populations should be advanced F_3 and evaluated for their WUE and drought tolerance. Screening for water use efficie y and drought tolerance in wheat genotypes is vital for selecting wheat genotypes with higher grain yield, drought tolerance and WUE for selection, genetic advancement and production. Cultivating water-use-effici t wheat cultivars will contribute to yield stability to achieve food security, economic opportunities and enhanced livelihoods.

Therefore, the objective of the present study is to determine the agronomic performance and WUE of newly bread wheat populations under drought-stressed and non-stressed conditions to select water use efficient and drought-tolerant families for genetic advancement and production.

2 Materials and methods

2.1 Plant materials

Eight wheat genotypes obtained from the International Maize and Wheat Improvement Centre (CIMMYT) heat and drought nursery were selected from a panel of 100 diverse genotypes [19] and two local checks adapted to dryland wheat production in South Africa (Table 1). The genotypes were selected for their desirable root-to-shoot biomass allocation and yield advantage under water-limited growing conditions. Additional information on the original panel and the selection process can be found in Mathew et al. [19]. The 10 selected genotypes were used as breeding parents and crossed in a full diallel mating design to generate 90 F_1 populations [20]. Seed from each family was bulked and selfed over two generations to generate 90 F_2 families. Advancing both direct and reciprocal crosses was justified because o reports on the presence of maternal effects for root biomass and abiotic stress tolerance in wheat [19, 21]. A total of 100 genotypes consisting of the ten parental lines and 90 F_3 families were evaluated in the present study under drought-stressed and non-stressed conditions.

2.2 Experimental site description

The 100 genotypes were evaluated at the Ukulinga Research Farm (latitude: 29.667^0 longitude: 30.406^0 and altitude: 811) located in Pietermaritzburg, in the KwaZulu-Natal province of South Africa, over two seasons (2022 and 2023). The Ukulinga Research Farm is the experimental farm for the University of KwaZulu-Natal (UKZN), Pietermaritzburg Campus. The area is classified as semi-arid, has warm to hot summer months and cool winters with a long-term (10 years) average temperature of 26.5 °C [22]. The annual average rainfall is 738 mm, and most of the rain falls during the summer months (October–April), with ~ 20% falling during the winter months [23]. Detailed meteorological data of the experimental site during the 2022 and 2023 growing seasons were recorded in Table 2. The soil at the experimental site was clay-to-loamy clay, acidic, shallow, and had low fertility [22]. The soil properties of the experimental area are given in Table 3.

2.2.1 Trial establishment and layout

Two experiments were conducted under field conditions at Ukulinga Research Farm. The first trial was conducted from July to November 2022, and the second from August to December 2023. The field was ploughed to a depth of 30 cm and harrowed to ensure fine tilth for optimal germination. Basal fertilizer was applied at 120, 30, and 30 kg ha^{-1} of nitrogen, phosphorous, and potassium, respectively. The trials were laid out in a 5 × 20 alpha lattice design with two replicates

Table 1 List of wheat parents used to generate wheat populations

Parental Genotypes	Pedigree
LM26	ATTILA * 2/PBW65//TAM200/TUI
LM47	FRET2/KUKUNA//FRET2/3/YANAC/4/FRET2/KIRITATI
LM48	FRET2/KUKUNA//FRET2/3/PASTOR//HXL7573/2 *BAU/5/FRET2 *2/4/SNI/TRAP#1/3/KAUZ * 2/TRAP//KAUZ
LM71	BABAX/3/PRL/SARA//TSI/VEE#5/4/CROC_1/AE.SQUARROSA (224)//2 * OPATA
LM75	BUC/MN72253//PASTOR
BW141	CGSS05B00243T-099TOPY-099 M-099NJ-099NJ-1WGY-0B
BW152	CGSS05B00258T-099TOPY-099 M-099NJ-1WGY-0B
BW162	CGSS05B00304T-099TOPY-099 M-099NJ-099NJ-3WGY-0B
LM70	Local check
BW140	Local check

Table 2 Weather conditions at Ukulinga Research Farm during the growing periods

Month	Rain	Tmax	Tmin	Rhmax	Rhmin
July—November 2022					
July	5.8	22.8	10	83.2	50.3
August	8.1	22.4	9.8	88.4	61.9
September	20.6	26.1	13.4	84.1	40.2
October	39.1	26.3	15.3	90.5	38.2
November	72.6	23.9	15	94	32.8
August—December 2023					
August	6.8	21.8	10	88.6	49.6
September	7.3	22.7	12.4	84.2	62.3
October	33.1	25.1	13.6	88.3	39.5
November	63.2	22.9	15.6	91.3	32.9
December	77.2	24.6	14.6	94	33

Rain = rainfall (mm); T_{max} = maximum temperature (°C); T_{min} = minimum temperature (°C); Rh_{max} = maximum relative humidity (%); Rh_{min} = minimum relative humidity (%)

Table 3 Soil properties for the environment used in this study

Properties	Field conditions
Bulk density (g cm^{-3})	1.04
Phosphorus (mg/l)	39
Potassium (mg/l)	241
Nitrogen (%)	0.23
Calcium (mg/l)	1453
Magnesium (mg/l)	369
Ph	4.56
Clay%	28
Organic Carbon (%)	2.6
Electrical Conductivity	11.02

per treatment. The soil on the experimental area was covered with a custom-made black plastic mulch rainout shelter system to avoid rainfall infilt ation into the soil profil . Small holes measuring ~ 5 cm in diameter were drilled on the black plastic mulch along the planting rows. The plot size was a 1 m-long plot with an inter-row spacing of 30 cm and intra-row spacing of 20 cm. Three wheat seeds were planted at each hole and thinned out after two weeks to leave two plants per hole. The border rows were used to reduce the risk of yield infl tion in test plots in the outer rows. Two water regimes (drought-stressed (DS) and non-stressed (NS)) were laid out adjacent to each other, and an automatic drip irrigation system was used to apply water in both water regimes. Each row had a dripper line running below the custom-made plastic mulch for precision and automated water application. Rainwater that may enter or seep through the holes was negligible as the holes were covered by the plant canopy as the plants grew.

2.2.2 Irrigation water management

The plants in both treatments were irrigated equally until water stress was imposed into the drought-stressed treatment by withholding irrigation to 35% field capacity from 50% heading to physiological maturity. This was done in order to mimic terminal drought stress. In the non-stressed treatment, adequate irrigation continued until the plants reached physiological maturity (Fig. 1). The water sensors (HOBO UX120, Onset, Bourne, MA, USA) was used to determine fiel capacity under both water regimes.

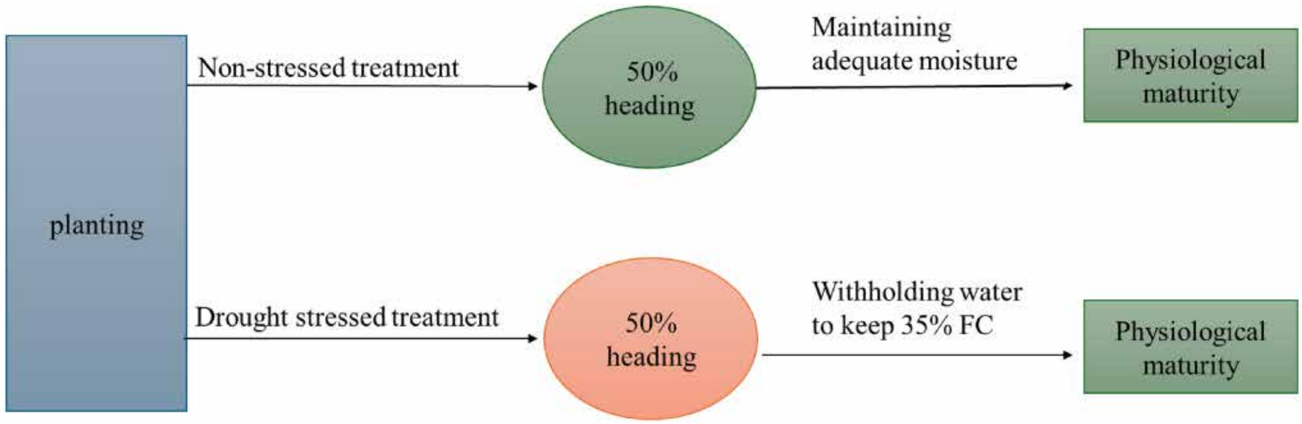

Fig. 1 Scheme of irrigation water application in the drought-stressed and non-stressed treatments. FC = field capaci y

2.3 Data collection

2.3.1 Phenotyping yield and yield components

During the two growing periods, data for phenotypic traits was recorded. The traits recorded before harvesting were number of days to 50% heading (DTH), which was recorded as the number of days from the date of sowing to the date when 50% of the plants in a plot had fully emerged spikes from the flag leaf, whilst number of days to 50% maturity (DTM) was recorded as the number of days from the date of sowing to the date when 50% of the plant in a plot had dried spikes. Plant height (PH) was recorded in centimetres as an average measurement of three randomly selected plants from the soil surface to the tip of the spike after the plants reached physiological maturity. The number of productive tillers (TN) per plant was measured as the average number of the counted tillers from three stations (with 2 plants per station).

After harvesting, the spike length (SL) was measured in centimetres from the base of the spike to the tip of a fully developed spike, and the number of spikelets per spike (SPS) were counted and recorded as the mean of three randomly selected spikes per plot. Spike weight (SW) was measured by weighing all the spikes produced in a plot on a weighing balance and was expressed in g m^{-2}. Grain yield (GY) was measured as the weight of the grain produced per genotype and expressed in g m^{-2}.

2.3.2 Determination of root and shoot biomass variables

Shoot biomass (SB) was measured after harvesting, and shoots were dried at 70 °C for 48 h to measure the dry weight of the shoots without the spikes and normalized to g m^{-2}. The root biomass (RB) was measured following the methodology by Mathew et al. [19] with slight modific tion. Briefl , a 20 × 20 × 20 cm sampling box was sunk to a depth of 60 cm, and all the roots within the soil volume were collected per genotype per plot. The larger roots were manually separated from the soil, and the finer roots were collected by wet sieving through a 2 mm sieve added to the larger roots. The roots were oven-dried at 70 °C for 48 h to measure the dry weight of the roots and the units were normalized to g m^{-2}. The total plant biomass (PB) was calculated as a sum of the spike weight, shoot biomass and root biomass and recorded in g m^{-2}. Root-to-shoot ratio was calculated as the ratio of the root biomass to shoot biomass. The harvest index was calculated using the equation [21] posed by Shamuyarira et al. [20]:

$$HI = \frac{GY}{GY + SB} \times 100 \tag{1}$$

where HI = harvest index; GY = grain yield produced in g m^{-2}; SB = shoot biomass in g m^{-2}.

2.3.3 Determination of irrigation water use efficiency

The irrigation water use efficie y for grain yield (WUE_{gy}), shoot biomass (WUE_{sb}), root biomass (WUE_{rb}) and total plant biomass (WUE_{pb}) were calculated following the formulae proposed by Jing et al. [24] and Hussain et al. [25]:

$$WUE_{gy} = \frac{GY}{\text{amount of water applied}} \quad (2)$$

Where GY = grain yield produced in g m^{-2}, WUE_{gy} = grain yield water use efficie y.

$$WUE_{sb} = \frac{SB}{\text{amount of water applied}} \quad (3)$$

Where SB = shoot biomass in g m^{-2}, WUE_{sb} = shoot biomass water use efficie y.

$$WUE_{rb} = \frac{RB}{\text{amount of water applied}} \quad (4)$$

Where RB = root biomass in g m^{-2}, WUE_{rb} = root biomass water use efficie y.

$$WUE_{pb} = \frac{PB}{\text{amount of water applied}} \quad (5)$$

WUE_{pb} = total plant water use efficie y; PB = total plant biomass in g m^{-2}

2.3.4 Drought stress indices

The following drought stress indices were calculated to assist the selection of drought tolerant families: drought susceptibility index (DSI), geometric mean productivity (GMP), harmonic mean (HM), mean productivity (MP), stress susceptibility index (SSI) stress tolerance index (STI), tolerance index (TOL), yield index (YI) and yield stability index (YSI) [26–32]:

$$\text{Drought susceptibility index} = \frac{Ys - Yp}{Yp} \quad (7)$$

$$\text{Geometric mean productivity} = (\text{Yp} \times \text{Ys})^{\frac{1}{2}} \quad (8)$$

$$\text{Harmonic mean} = \frac{2(Ys \times Yp)}{Yp + Ys} \quad (9)$$

$$\text{Mean productivity} = \frac{Yp + Ys}{2} \quad (10)$$

$$\text{Stress Susceptibility Index} = \frac{\left(1 - \frac{Y_s}{Y_p}\right)}{\left(1 - \frac{\overline{Y}_s}{\overline{Y}_p}\right)} \quad (11)$$

$$\text{Stress tolerance index} = \frac{Yp \times Ys}{\overline{Y}_p^2} \quad (12)$$

$$\text{Tolerance index} = Y_p - Y_s \tag{13}$$

$$\text{Yield index} = \frac{Ys}{\overline{Y}_s} \tag{14}$$

$$\text{Yield stability index} = \frac{Ys}{Yp} \tag{15}$$

where Y_p is the mean yield of the genotype under non-stressed conditions, Y_s is the mean yield of the genotype under stress conditions, $\overline{Y}_p$ is the mean yield of all genotypes under non-stressed conditions, and $\overline{Y}_s$ is the mean yield of all genotypes under drought-stressed conditions.

2.4 Data analysis

Summary statistics describing mean, minimum, maximum, quartile 1 (25%), quantile 3 (75%), standard deviation, standard error of the mean, coeffici t of variation (%CV), skewness (skew), and kurtosis (Kurt) were generated using IBM SPSS statistical software version 28 for all the agronomic traits and water use efficie y variables (WUE_{gy}, WUE_{sb}, WUE_{rb} and WUE_{pb}). The two seasons' data for agronomic traits and water use efficie y variables was subjected to a combined analysis of variance (ANOVA) following the lattice procedure in GenStat 23rd edition [33] by considering genotypes, seasons, and water regimes as fi ed factors. The comparisons of means were done using Fisher's least significa t difference at the 5% significance level. The drought stress indices were computed based on the gain yield produced under DS and NS conditions using calculated using IBM SPSS statistical software.

3 Results

3.1 Climatic conditions during the two growing seasons

The total amount of rainfall during the 2022 and 2023 growing seasons was 146.2 mm and 187.6 mm, respectively (Table 2). Mean temperatures during the first growing season was varied with a minimum of 12.7 °C and a maximum of 24.3 °C. During the second growing season, the mean maximum temperature (23.42 °C) was slightly lower than the maximum temperature during the first growing season (24.3 °C) (Table 2).

4 Summary statistics

An overview of the variations of agronomic traits and water use efficie y (WUE) variables for all 100 wheat genotypes across the two seasons and two water regimes is presented in Table 4. The root biomass (RB) has a relatively higher %CV (57.55%) than any other agronomic recorded, indicating that the RB values have the highest variations across the two treatments and seasons. Among all the recorded agronomic traits, only plant height (PH) has a negative skewness value (-1.08), meaning that the values were skewed to the left. The WUE_{sb} was widely varied across treatments and seasons, as indicated by a minimum value of 0.04 g mm^{-1} and a maximum value of 1.73 g mm^{-1} (Table 4).

4.1 Effects of genotype, season, water regime and their interactions on phenotypic traits and water use efficiency

The combined analysis of variance with mean squares and significa t tests for agronomic traits and water use efficie y for the evaluated genotypes is presented in Table 5. The genotype effects were significa t ($p < 0.05$) for agronomic traits and water use efficiency variables. The interaction between genotype and water regime had signifi ant ($p < 0.05$) effects on DTH, SW, GY and WUE_{gy}, and was non-significant on DTH, SPS and PH. In addition, the effect of genotype x season interaction was significa t on DTM, PH, TN, RB, HI and WUE_{rb}, but was non-significa t on DTM, SL, SPS, SW, GY, SB, PB, RS, WUE_{gy}, WUE_{sb} and WUE_{pb}. The season x genotype x treatment interaction effect was non-significa t for agronomic traits and water use efficie y variables (Table 5).

Table 4 Summary statistics of agronomic traits and water use efficie y variables measured in 100 wheat genotypes across seasons and water regimes

Variables	DTH	DTM	PH	TN	SL	SPS	SW	GY	SB	RB	R:S	HI	PB	WUE_{gy}	WUE_{sb}	WUE_{rb}	WUE_{pb}
Mean	64.24	99.69	80.57	4.59	9.71	9.61	931.51	491.44	1514.09	266.72	0.19	19.65	2711.46	0.12	0.37	0.07	0.63
Minimum	57.00	89.00	7.80	1.10	2.30	0.50	53.33	26.67	155.56	22.22	0.01	1.47	368.89	0.01	0.04	0.01	0.10
Maximum	74.00	108.00	109.30	15.00	110.00	52.00	3466.67	1500.00	6600.00	911.11	0.45	60	8146.67	0.39	1.73	0.24	2.13
Quartile 1	63.00	97.00	75.80	3.60	8.60	6.50	586.67	266.67	1177.78	155.56	0.11	13.21	2078.33	0.06	0.28	0.04	0.48
Quartile 3	66.00	101.00	85.50	5.30	10.50	11.33	1184.43	650.00	1800.00	343.33	0.25	24.99	3234.44	0.16	0.44	0.09	0.75
Standard deviation	9.85	14.77	14.30	1.74	4.15	5.54	504.69	301.14	648.97	153.51	0.09	9.12	1053.16	0.07	0.16	0.04	0.25
Standard error of mean	0.09	0.12	0.28	0.06	0.14	0.19	17.36	10.45	21.77	5.30	0.00	0.31	34.8	0.00	0.01	0.00	0.01
Coeffici t of variation (%)	15.33	14.82	17.76	37.99	42.71	57.70	54.18	61.28	42.86	57.55	49.75	46.43	38.84	60.06	44.22	57.54	39.38
Skewness	0.26	0.35	−1.08	1.36	21.38	3.48	1.33	0.77	2.31	1.19	0.59	0.55	1.06	0.71	2.70	1.22	1.41
Kurtosis	1.01	−0.47	9.72	5.65	545.73	19.76	3.39	0.03	15.29	1.49	−0.26	0.68	3.3	0.01	19.13	1.91	5.8

DTM = days to 50% heading, DTM = days to 50% maturity, PH = plant height in centimetres, TN = number of productive tillers per plant, SL = spike length in centimetres, SPS = spikelets per spike, SW = spike weight (g m^{-2}), GY = grain yield (g m^{-2}), SB = shoot biomass (g m^{-2}), RB = root biomass (g m^{-2}), PB = total plant biomass (g m^{-2}), HI = harvest index, R:S = root-to-shoot ratio, WUE_{gy} = grain yield water use efficie y (g mm^{-1}), WUE_{sb} = shoot biomass water use efficie y (g mm^{-1}), WUE_{rb} = root biomass water use efficie y (g mm^{-1}), WUE_{pb} = total plant biomass water use efficie y (g mm^{-1})

Table 5 Mean squares for agronomic traits and water use efficie y variable for all the 100 wheat genotypes evaluated across two seasons and two water regimes (drought-stressed and non-stressed)

Source of variation	df	DTH	DTM	PH	TN	SL	SPS	SW	GY
Block	4	5.767	15.41	219.31**	3.963	16.36	93.53**	271,769.00	194,324.00*
Rep	1	67.972***	9.55	1933.54***	21.239**	19.19	0.24	235,396.00	112,706.00
Season (S)	1	1.127	5.71	930.57***	65.422***	53.61	0.16	6,796,162.00***	4,539,750.00***
Genotype (G)	99	7.748***	12.50*	69.10*	2.777*	18.27**	29.97*	250,066.00*	85,171.00**
Water regime (W)	1	74.961***	5.28	227.76*	5.261	0.001	5.46	5,452,968.00***	2,387,186.00***
S x G	98	8.998***	13.10	74.87*	3.423**	16.74	35.58	272,339.00	89,618.00
S x W	1	0.177	0.55	401.40**	8.648	41.46	24.30	7,378,439.00***	5,740,226.00***
G x W	99	6.685*	10.74	47.12*	2.430*	15.75*	29.61*	176,098.00*	56,528.00*
S x G x W	97	5.944	8.66	47.37	2.797	14.83	26.24	145,106.00	44,139.00
Residual	380	4.774	11.08	56.52	2.155	14.32	27.87	221,955.00	72,517.00
Total	781	6.234	11.16	63.11	2.636	15.46	29.35	241,034.00	87,332.00
Source of variation	**SB**	**RB**	**PB**	**R:S**	**HI**	**WUE_{gy}**	**WUE_{sb}**	**WUE_{rb}**	**WUE_{pb}**
Block	396,919.00	13,825.00	750,409.00	0.008147	138.17	0.010548*	0.02665	0.000788	0.05436
Rep	804,328.00	49,458.00	2,653,257.00	0.001802	0.02	0.003934	0.05131	0.002897	0.12993
Season (S)	13,227,370.00***	1,130,044.00***	26,590,234.00***	1.393323***	1270.20***	0.231637***	0.84611***	0.066164***	0.20268
Genotype (G)	560,649.00***	28,260.00*	1,371,321.00***	0.005751**	84.40*	0.005078**	0.03420**	0.001674*	0.08087***
Water regime (W)	18,198.00	13,275.00	6,539,999.00**	0.002458	1362.19***	0.020927*	0.49123***	0.009633**	2.09281***
S x G	375,367.00	26,978.00*	1,082,363.00	0.007519	84.34*	0.005323	0.02306	0.001585*	0.06007
S x W	240,935.00	12,599.00	4,329,832.00*	0.000775	5738.30***	0.302136***	0.02630	0.000079	0.12720
G x W	225,964.00	17,870.00	591,580.00	0.006002	49.86	0.003342*	0.01429	0.001060	0.03082
S x G x W	363,062.00	16,000.00	832,040.00	0.005681	67.09	0.002651	0.02221	0.000926	0.04296
Residual	343,206.00	19,879.00	875,358.00	0.006154	59.80	0.004297	0.02156	0.001183	0.04936
Total	379,225.00	22,506.00	969,088.00	0.007965	76.46	0.004924	0.02424	0.001341	0.05460

***P < 001, **P < 0.01, * P < 0.05

df = degrees of freedom, Rep = replication, DTM = days to 50% heading, DTM = days to 50% maturity, PH = plant height in centimetres, TN = number of productive tillers per plant, SL = spike length in centimetres, SPS = spikelets per spike, SW = spike weight (g m^{-2}), GY = grain yield (g m^{-2}), SB = shoot biomass (g m^{-2}), RB = root biomass (g m^{-2}), PB = total plant biomass (g m^{-2}), HI = harvest index, R:S = root-to-shoot ratio, WUE_{gy} = grain yield water use efficie y (g $plot^{-1}$ mm^{-1}), WUE_{sb} = shoot biomass water use efficie y (g mm^{-1}), WUE_{rb} = root biomass water use efficie y (g mm^{-1}), WUE_{pb} = total plant water use efficie y (g mm^{-1}), S = season; G = genotype, W = water regime

Table 6 Mean values for yield components, root attributes and water use efficie y of the top 10 and bottom 5 wheat parental lines and F3 populations evaluated in two seasons ranked based on grain yield water use efficie y under drought-stressed conditions

Genotype	DTH		DTM		PH		TN		SL		SPS		SW		GY		SB	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Top 10 genotypes																		
BW141 X LM71	64.25	63.50	98.5	99.25	86.3	88.03	5.08	5.85	36.35	10.61	11.04	10.46	1558.89	1930.00	800.00	823.33	1983.33	2152.78
LM71 X BW162	64.25	65.00	101.25	100.25	75.4	75.23	5.50	6.05	8.08	10.03	10.71	7.99	1255.56	970.00	726.11	908.33	1602.78	1638.89
BW140 X LM70	63.00	63.50	99.25	97.75	83.03	79.3	5.70	4.78	9.12	9.61	10.43	6.85	1290	833.33	699.17	800.00	1881.11	1767.22
BW162 X BW140	62.50	64.50	97.75	99.50	82.90	77.9	4.53	5.13	8.43	9.63	9.88	9.98	1176.67	1602.22	687.5	823.61	1538.89	1361.11
BW141 X LM26	62.00	63.75	95.00	101.00	77.90	80.55	4.30	3.80	9.45	9.96	13.31	9.04	1131.11	823.33	643.06	769.44	1458.33	1063.89
BW162 X LM71	62.50	64.25	98.25	102.25	78.10	82.55	5.10	4.30	9.26	9.65	7.56	9.6	1276.67	1020	629.17	840.83	1546.11	1532.78
BW152 X LM71	64.50	63.25	103.50	100.25	79.55	79.05	5.28	4.65	9.36	9.75	8.1	10.22	1172	1040.36	618.33	770.79	1383.33	1647.22
LM70 X BW141	62.00	64.25	97.50	98.25	83.13	80.05	4.98	6.08	9.59	9.52	18.75	6.4	976.67	1070	617.5	810	2552.78	1866.11
LM75 X LM47	67.00	64.00	103.5	99.25	79.38	76.58	4.88	4.55	9.5	9.31	11.5	9.45	1082.22	1013.33	598.89	790.83	1505	834.44
LM70 X BW140	62.75	65.25	97.75	102.5	86.48	89.53	5.35	4.98	8.87	9.68	8.50	8.65	1152.22	773.33	590	760.06	1808.33	1631.67
Bottom 5 genotypes																		
LM26	65.33	66.33	102.00	103.67	70.60	79.73	5.00	5.00	9.26	8.67	7.07	9.23	367.41	1177.78	216.07	443.33	1333.33	1288.89
BW140 X BW141	62.50	63.75	98.25	98.25	80.95	76.28	4.70	3.85	7.56	8.78	9.13	8.07	478.22	1026.10	198.61	637.78	1005.56	1458.33
LM71	63.25	65.5	101.25	100.75	84.65	75.28	4.55	3.83	9.11	9.98	8.90	9.00	956.67	980.00	184.72	466.67	1211.11	1405.56
LM47 X LM70	64.75	64.25	97.75	94.00	82.13	78.25	4.83	5.18	9.06	9.80	8.65	6.20	503.33	993.33	183.33	427.50	1513.89	1633.89
BW141	65.33	65.5	102.33	97.50	83.58	78.3	3.83	3.58	8.02	9.60	7.17	6.04	383.70	976.67	131.48	460.00	925.93	1058.33
Mean	63.94	64.56	99.78	99.63	81.01	80.02	4.69	4.50	9.69	9.69	9.68	9.53	844.00	1008.11	427.67	589.71	1499.45	1512.94

Table 6 (continued)

Genotype	DTH		DTM		PH		TN		SL		SPS		SW		GY		SB	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Std	1.31	1.40	1.82	1.67	4.40	3.41	0.86	0.80	2.82	0.87	3.07	2.54	212.16	261.35	125.04	144.13	356.90	283.09
%CV	2.06	2.17	1.82	1.68	5.43	4.26	18.37	17.74	29.05	9.02	31.7	26.69	25.14	25.93	29.24	24.44	23.80	18.71
SEM	0.13	0.14	0.18	0.17	0.44	0.34	0.09	0.08	0.28	0.09	0.31	0.25	21.11	26.00	12.44	14.34	35.51	28.17
LSD (5%)	3.08	3.52	4.78	4.43	12.67	9.09	2.55	1.97	1.04	2.87	1.16	9.39	85.17	101.70	50.90	55.62	36.50	94.60
Genotype	SB		RB		R:S		HI		PB		WUE_{gy}		WUE_{sb}		WUE_{rb}		WUE_{pb}	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Top 10 genotypes																		
BW141 X LM71	1983.33	2152.78	250.00	365.56	0.15	0.17	21.2	20.24	3792.22	4448.33	0.21	0.19	0.52	0.49	0.07	0.08	0.99	0.91
LM71 X BW162	1602.78	1638.89	332.22	397.78	0.21	0.24	31.04	22.6	3190.56	3006.67	0.19	0.21	0.42	0.37	0.09	0.09	0.83	0.66
BW140 X LM70	1881.11	1767.22	330.00	318.89	0.2	0.17	20.57	16.59	3501.11	2919.44	0.18	0.18	0.49	0.4	0.09	0.07	0.92	0.64
BW162 X BW140	1538.89	1361.11	271.11	261.11	0.18	0.21	25.13	26.41	2986.67	3224.44	0.18	0.19	0.4	0.31	0.07	0.06	0.78	0.66
BW141 X LM26	1458.33	1063.89	288.89	183.33	0.18	0.19	23.18	23.3	2878.33	2070.56	0.17	0.18	0.38	0.24	0.08	0.04	0.75	0.43
BW162 X LM71	1546.11	1532.78	186.67	274.44	0.13	0.18	22.75	20.46	3009.44	2827.22	0.16	0.19	0.4	0.35	0.05	0.06	0.79	0.58
BW152 X LM71	1383.33	1647.22	264.44	394.53	0.22	0.24	25.26	27.36	2819.78	3082.11	0.16	0.18	0.36	0.37	0.07	0.09	0.74	0.67
LM70 X BW141	2552.78	1866.11	241.11	464.44	0.18	0.24	18.74	21.03	3770.56	3400.56	0.16	0.18	0.67	0.42	0.06	0.11	0.99	0.74
LM75 X LM47	1505	834.44	230	187.78	0.17	0.26	23.25	26.68	2817.22	2035.56	0.16	0.18	0.39	0.19	0.06	0.04	0.74	0.39
LM70 X BW140	1808.33	1631.67	424.44	323.33	0.22	0.2	17.26	17.07	3385	2728.33	0.15	0.14	0.47	0.37	0.11	0.07	0.88	0.58
Bottom 5 genotypes																		
LM26	1333.33	1288.89	140.74	155.56	0.11	0.20	12.42	18.3	1841.48	2622.22	0.06	0.10	0.35	0.29	0.04	0.04	0.48	0.47

Table 6 (continued)

Genotype	SB		RB		R:S		HI		PB		WUE_{gy}		WUE_{sb}		WUE_{rb}		WUE_{pb}	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
BW140 X BW141	1005.56	1458.33	188.89	197.42	0.22	0.16	12.46	25.48	1672.67	2681.86	0.05	0.15	0.26	0.33	0.05	0.04	0.44	0.55
LM71	1211.11	1405.56	233.33	311.11	0.22	0.22	11.26	18.39	2401.11	2696.67	0.05	0.11	0.32	0.32	0.06	0.07	0.63	0.55
LM47 X LM70	1513.89	1633.89	305.56	295.56	0.21	0.17	9.20	16.45	2322.78	2922.78	0.05	0.10	0.40	0.37	0.08	0.07	0.61	0.62
BW141	925.93	1058.33	117.04	166.67	0.17	0.17	14.96	21.76	1426.67	2201.67	0.03	0.10	0.24	0.24	0.03	0.04	0.37	0.41
Mean	1499.45	1512.94	260.65	270.58	0.19	0.18	18.32	20.92	2608.1	2791.62	0.11	0.13	0.39	0.34	0.07	0.06	0.68	0.58
Std	356.90	283.09	73.44	80.61	0.04	0.04	3.85	4.44	529.08	489.26	0.03	0.03	0.09	0.06	0.02	0.02	0.14	0.10
%CV	23.80	18.71	28.18	29.79	20.65	21.32	21.03	21.23	20.29	17.53	29.2	24.42	23.75	18.65	28.18	29.79	20.29	17.75
SEM	35.51	28.17	7.31	8.02	0.00	0.00	0.38	0.44	52.64	48.68	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01
LSD (5%)	36.50	94.60	3.04	28.99	0.02	0.02	1.58	1.52	197.60	173.40	0.01	0.01	0.04	0.02	0.01	0.01	0.05	0.04

DS = drought stress, NS = non drought stress, DTM = days to 50% heading, DTM = days to 50% maturity, PH = plant height in centimetres, TN = number of productive tillers per plant, SL = spike length in centimetres, SPS = spikelets per spike, SW = spike weight (g m^{-2}), GY = grain yield (g m^{-2}), SB = shoot biomass (g m^{-2}), RB = root biomass (g m^{-2}), PB = total plant biomass (g m^{-2}), HI = harvest index, R:S = root-to-shoot ratio, WUE_g = grain yield water use efficie y (g mm^{-1}), WUE_{sb} = shoot biomass water use efficie y (g mm^{-1}), WUE_{rb} = root biomass water use efficie y (g mm^{-1}), WUE_{pb} = total plant biomass water use efficie y (g mm^{-1})

Table 7 Mean grain yield and drought stress indices of the top 10 and bottom 5 genotypes evaluated across the two experimental test sites under drought-stressed and non-stressed conditions, ranked based on grain yield production under drought-stressed conditions

Genotype	Y_s	R	Y_p	R	MP	R	GMP	R	SSI	R	TOL	R	YI	R	YSI	R	HM	R	DSI	R	STI	R	Mean Rank
Top 10 genotypes																							
BW141 X LM71	800.00	1	823.33	6	811.67	2	40.29	2	0.09	97	23.33	94	24.61	1	0.97	4	811.50	1	−0.03	4	283.87	2	23.00
LM71 X BW162	726.11	2	908.33	1	817.22	1	40.43	1	0.62	60	182.22	38	22.34	2	0.80	41	807.06	2	−0.20	41	284.25	1	20.78
BW140 X LM70	699.17	3	800.00	9	749.58	4	38.72	4	0.39	79	100.83	66	21.51	3	0.87	22	746.19	4	−0.13	22	241.06	4	23.11
BW162 X BW140	687.50	4	823.61	5	755.56	3	38.87	3	0.51	68	136.11	54	21.15	4	0.83	33	749.43	3	−0.17	33	244.03	3	22.67
BW141 X LM26	643.06	5	769.44	14	706.25	7	37.58	7	0.51	69	126.39	58	19.78	5	0.84	32	700.60	7	−0.16	32	213.24	7	24.89
BW162 X LM71	629.17	6	840.83	3	735.00	5	38.34	5	0.77	44	211.67	29	19.35	6	0.75	57	719.76	5	−0.25	57	227.99	5	23.67
BW152 X LM71	618.33	7	770.79	13	694.56	9	37.27	9	0.61	61	152.46	49	19.02	7	0.80	40	686.20	8	−0.20	40	205.40	8	25.67
LM70 X BW141	617.50	8	810.00	7	713.75	6	37.78	6	0.73	54	192.50	33	18.99	8	0.76	47	700.77	6	−0.24	47	215.56	6	23.67
LM75 X LM47	598.89	9	790.83	10	694.86	8	37.28	8	0.75	51	191.94	34	18.42	9	0.76	50	681.61	9	−0.24	50	204.12	9	25.33
LM70 X BW140	590.00	10	760.06	16	675.03	10	36.74	10	0.69	57	170.06	43	18.15	10	0.78	44	664.32	10	−0.22	44	193.26	10	26.44
Bottom 5 genotypes																							
LM26	216.07	96	443.33	86	329.70	92	25.68	92	1.58	10	227.26	26	6.65	96	0.49	91	290.54	94	−0.51	91	41.28	93	76.11
BW140 X BW141	198.61	97	637.78	38	418.19	78	28.92	78	2.12	2	439.17	2	6.11	97	0.31	99	302.90	92	−0.69	99	54.59	88	70.56
LM71	184.72	98	466.67	81	325.69	93	25.52	93	1.86	5	281.94	15	5.68	98	0.40	96	264.68	96	−0.60	96	37.15	94	76.22
LM47 X LM70	183.33	99	427.50	90	305.42	95	24.72	95	1.76	6	244.17	25	5.64	99	0.43	95	256.62	97	−0.57	95	33.78	96	78.11
BW141	131.48	100	460.00	82	295.74	96	24.32	96	2.20	1	328.52	12	4.04	100	0.29	100	204.51	100	−0.71	100	26.07	99	78.22

Y_p = grain yield under non-stressed conditions (in g m^{-2}); Y_s = grain yield under drought-stressed conditions (in g m^{-2}); R = rank; SSI = stress susceptibility index; GMP, geometric mean productivity; MP = mean productivity; HM = harmonic mean; TOL = stress tolerance index; STI = stress tolerance index; YI = yield index; YSI = yield stability index

4.2 Mean performance of wheat genotypes

The mean agronomic performances of the top 10 and bottom 5 performing wheat genotypes under drought-stressed and non-stressed conditions are presented in Table 6. The overall mean days to 50% heading (DTH) was lower under drought-stressed (64.03 days) than in non-stressed (64.39 days) (Table S1). Among the F_3 wheat populations, LM26 X LM70, LM47 X BW140, LM47 X BW162 were the early flowering under drought stress with the mean DTH of 61.00, 61.00 and 61.75 days, respectively, whilst under non-stressed the LM70 X BW141, BW141 X LM47 and LM71 X BW140 were the early flowering genotypes with the mean DTM of 61.25, 61.50 and 62.00 days, respectively. The days to 50% maturity (DTM) of the earliest maturing genotypes under drought stress included LM26 X BW140 and LM48 X BW141 and reached DTM at 95.00 and 95.25 days, respectively, whilst under non-stressed, the genotypes LM47 X LM70 and BW152 X LM70 reached DTM at 94.00 and 95.67 days, respectively (Table S1). The overall mean for plant height (PH) was higher under drought stress (81.09 cm) than non-stressed (80.43 cm). The SPS for the evaluated genotypes ranged from 5.58 (LM71 X LM75) to 21.65 (LM71 X BW152) under drought stressed, whilst under non-stressed it ranged from 6.04 (BW141) and 18.27 (BW162 X LM48) (Table S1).

The grain yield (GY) for the evaluated wheat genotypes was highly variable under drought-stressed conditions, with a minimum of 131.48 g m^{-2} recorded on BW141 and 800.00 g m^{-2}, which was observed on BW141 X LM71, whilst under non-stressed, GY was ranged from 245.83 g m^{-2} (LM75 X LM71) to 908.33 g m^{-2} (LM71 X BW162) (Table S1). Among the parental lines, the highest GY under drought-stressed and non-stressed conditions was exhibited by LM48 with 504.17 g m^{-2} and 774.17 g m^{-2}, whilst BW141 had the lowest grain yield under drought-stressed (131.48 g m^{-2}) and BW162 had the lowest grain yield under non-stressed (343.89 g m^{-2}) (Table S1). The mean GY for all wheat genotypes was higher under non-stressed (654.28 g m^{-2}) than drought stress (518.01 g m^{-2}). In addition, under drought-stressed conditions, 21.11% of the F3 wheat populations produced high grain yield production than all the parental lines and under non-stressed conditions, 10% of F_3 wheat populations had higher grain yield than the parental lines (Table S1).

Furthermore, the results showed that mean shoot biomass was lower under drought-stressed (1499.45 g m^{-2}) than under non-stressed treatment (1512.94 g m^{-2}) (Table S1). The parental lines with the highest harvest index (HI) under drought-stressed were LM48 and BW140, with 23.45% and 20.47%, respectively, whilst under non-stressed, the highest HI was observed on BW140 and LM48, with 32.09% and 25.35%, respectively. Mean HI for wheat genotypes was reduced by 4.91% under drought stress. On average, root biomass (RB) was 270.58 g m^{-2} under non-stressed conditions, which was lower than 260.65 g m^{-2} attained under drought-stressed conditions (Table S1). Overall, total plant biomass (PB) was reduced by 0.20% under drought-stressed. On average, the root-to-shoot ratio (R:S) of all parental lines and their crosses was slightly higher under drought-stressed (0.19) than in non-stressed conditions (0.18) (Table S1). The R:S varied from 0.11 (LM26) to 0.29 (BW152 X LM47) under a drought-stressed environment, whilst under non-stressed conditions, it ranged between 0.09 (LM75 X LM48) to 0.29 (LM47) (Table S1).

4.3 Irrigation water use efficiency

Results revealed that grain yield water use efficiency for F_3 wheat populations ranged between 0.05 g mm^{-1} which was observed in LM47 X LM70 and 0.21 g mm^{-1} recorded on BW141 X LM71 under drought-stressed, whilst under non-stressed the grain yield water use efficiency ranged from 0.05 g mm^{-1} which was recorded in LM75 X LM71 to 0.21 g mm^{-1} which was observed in LM71 X BW162 (Table 6 and Table S1). The parental lines with high grain yield water use efficiency under drought-stressed conditions were LM48 and BW140 with WUE_{gy} of 0.13 g mm^{-1} and 0.12 g mm^{-1}, respectively, whilst under non-stressed LM48 and LM70 with WUE_{gy} of 0.18 g mm^{-1} and 0.14 g mm^{-1}, respectively. On average, the shoot biomass water use efficiency was 0.43 g mm^{-1} under drought-stressed which was higher than 0.35 g mm^{-1} under non-stressed (Table S1). The %CV for WUE_{sb} was under drought-stressed was 21.96% which was higher than the non-stressed treatment (18.31%).

4.4 Comparison and selection of wheat populations based on tolerance indices and yield

After evaluating parental lines and their crosses for agronomic performance and water use efficiency under drought-stressed and non-stressed conditions. The different drought tolerance indices were further calculated to facilitate the identification and selection of the drought-tolerant or drought-susceptible wheat populations. The geometric mean productivity (GMP) and mean productivity (MP) indices were similar in categorizing the genotypes BW141 X LM71

(GMP = 40.29; MP = 811.67) and LM71 X BW162 (GMP = 40.43; MP = 817.22) as the most drought tolerant (Table 7 and Table S2), whilst categorizing the genotypes LM71 X LM48 (GMP = 22.73; MP = 258.33) and LM75 X LM71 (GMP = 21.70; MP = 235.42) as the most drought susceptible genotypes (Table 7 and Table S2). Among the parental lines, LM48 had an MP of 639.17 g m^{-2} which was higher whilst BW162 had the least MP of 281.39 g m^{-2}. According to the stress susceptibility index (SSI) and Tolerance (TOL) indices, LM75 X BW140 and LM26 X BW162 had the lowest TOL and SSI value which indicated that these two varieties have the highest drought tolerance. However, the LM75 X BW152 and BW140 X BW141 had the greatest TOL and SSI value among the F3 wheat populations, indicating that they are highly susceptible to drought stress (Table S2). The Drought stress tolerance index (STI) indicated that genotypes LM71 X BW141 (− 0.01), LM48 X BW140 (− 0.02) as the most drought tolerant genotypes and genotype BW140 X BW141 (-0.69) and LM75 X BW152 (-0.66) as the most susceptible wheat genotypes. Due to the lack of consistency of the drought indices in their ability to determine and select drought tolerant and susceptible wheat populations, the rank mean was calculated. The mean rank for the assessed drought indices was ranged from 20.78 (LM71 X BW162) to 79.67 recorded in BW162 (Table S2).

5 Discussion

5.1 Effects of drought stress on yield and yield-related components

The agronomic performance of all 100 wheat genotypes were varied across the treatments and seasons (Table 4). This agrees with Mwadzingeni et al. [34] and OlaOlorun et al. [3], who observed the phenotypic variations in wheat genotypes under drought-stressed and non-stressed conditions. According to Mathew et al. [19], the variations on agronomic performance of different wheat genotypes are as a result of genetic diversity. The significa t values of genotypes for DTH, DTM, TN, SPS, GY, SB, RB, PB and HI (Table 5), indicating that the tested parental lines and the families show genetic variations, which is useful during the selection for drought tolerance and water use efficie y using these agronomic traits. Furthermore, the main effect of water regime x season x genotype was non-significa t in all the evaluated yield and yield-related components. Similar results were found by Shamuyarira et al. [35], who reported that the main effect of water regime x season x genotype was non-significa t in all the evaluated yield and yield-related components.

The early maturing genotypes such as LM26 X BW140 (95.00 days) and LM48 X BW141 (95.25 days) are favoured in dry lands since they might avoid experiencing severe drought towards the end of their growth period and can potentially accommodate multiple cropping cycles due to their shorter duration. However, despite their shorter growth cycles, the early maturing genotypes are associated with reduced yields such as LM26 X BW140 (that was ranked 65th) (Table S1). These scenarios were reported by Mwadzingeni et al. [36] and Semahegn et al. [37], who found that early maturity genotypes were associated with low yields. Early maturity is a proxy trait for genotype selection with drought avoidance mechanism. The trade-off in early maturation is lost productivity due to reduced biomass production, root development, and shortened grain filling period. Mean grain yield for the assessed genotypes was lower under drought stress (427.67 g m^{-2}) than non-stressed conditions (589.71 g m^{-2}) (Table 6 and Table S1). That is in agreement with results were reported by Dorostkar et al. [38], who asserted that the mean grain yield for 36 evaluated wheat genotypes was higher under non-stressed than drought-stressed conditions. This is possibly because drought stress decreases the photosynthetic rate which results in poor of plant growth and development, which leads to a decrease in grain yield production [39].

Shoot biomass reduction of 0.89% under drought-stressed conditions was observed in this study because during drought stress, plants close their stomata to reduce water loss, which in turn limits carbon uptake leading to decreased biomass production. Gui et al. [40] also reported a decrease in shoot biomass due to the decrease in field capacity (FC) in the study conducted under 80% FC, 50% FC and 30% FC. Guasconi et al. [41], also asserted that drought stress negatively affects shoot biomass in all evaluated grass crops. Furthermore, the results showed that the mean HI under drought-stressed conditions was 18.32%, which was lower than the HI under non-stressed conditions, which was 20.92%. Indicating that these wheat genotypes were less effici t in converting biomass into harvestable yield under drought-stressed compared to non-stressed conditions. That is in agreement with Anwaar et al. [42] who reported a decrease in HI under drought conditions because both biological and grain yields decreased at different rates.

5.2 Impact of drought stress on irrigation water use efficiency

The WUE of wheat genotypes is seriously affected by water stress and various wheat genotypes respond differently to drought stress. The total plant water use efficie y for the evaluated wheat genotypes was varied across the water regime and seasons, with a minimum value of 0.10 g mm^{-1} and a maximum value of 2.13 g mm^{-1}. These findings align with Meena et al. [43], who reported a significa t variation in WUE of wheat genotypes under different irrigation treatments. The WUE_{gy} was not significa tly different for the interactions of water regime × season and genotype × water regime × season (Table 5), indicating that these genotypes had the ability to achieve optimum yield with limited applied water. These fi dings are consistent with Hussain et al. [25] who asserted similar results in water regime × season and genotype × water regime × season interactions on the WUE_{gy} of rice cultivars evaluated under drought-stressed and non-stressed conditions.

The results of the present study indicated that the WUE_{gy} was lower under drought-stressed (0.11 g mm^{-1}) than non-stressed conditions (0.13 g mm^{-1}) (Table S1). These results are supported by Yong'an et al. [17] and Boutraa et al. [18], who found a significa t decrease in WUE_{gy} under drought stress. The WUE of plants decreased under drought stress because of the high rates of transpiration and the crop cultivars may fail to produce optimum yields [12]. The WUE_{sb} was higher under drought-stressed than non-stressed conditions (Table 6), indicating that wheat genotypes have developed the mechanisms that allow them to use water they receive effici tly. These results align with the results of Mansour et al. [44], who found high biomass water use efficie y under lower irrigation and lower biomass water use efficie y under high irrigation. This suggests that high amounts of water applied to plants may lead to huge loss of water through transpiration which resulted in reduced shoot biomass water use efficie y. Under drought-stressed conditions, the overall mean of root biomass water use efficie y increased by 14.70% (Table S1). Similar results were demonstrated by Attia et al. [45], who found an increase in root biomass water use efficie y under drought-stress conditions. Therefore, the greater the amount of water applied resulted in water loss leading to reduced water use efficie y.

5.3 Comparison and selection of genotypes based on tolerance indices

Wheat genotypes, which are able to withstand water stress, normally use numerous strategies that vary with genotype based on their genetic makeup [46]. With regard to that, several authors have proposed several strategies that can be used to select the wheat genotypes based on their behaviour under drought stress such as drought stress indices. Drought tolerance indices are important criteria that assist in identifying drought tolerant wheat genotypes. The GMP and MP were the two drought stress indices which were equally effective at identifying drought tolerant and water use effici t wheat genotypes (Table 7 and Table S2). These results align with the results reported by Mohammadi et al. [47], who asserted that MP and GMP indices were more effective in identifying high yielding cultivars under water defici . However, the two selection indices SSI and TOL favoured wheat genotypes with high grain yield under drought stress and lower grain yield production under non-stressed conditions, which agreed with results reported elsewhere by Semahegn et al. [37], who asserted that SSI and TOL were favoured genotypes with high yields under drought stress conditions.

6 Conclusion

This study showed a wide variation in agronomic traits and WUE on the 100 evaluated wheat genotypes, indicating that these are vital genetic resources for the development of drought-tolerant and enhanced water use effici t varieties. The results showed that grain yield and WUE_{gy} were improved on the wheat population as compared to their parental lines under drought-stressed conditions. The drought indices such GMP, MP, HM, STI, YI, TOL, and SSI were better criteria for selecting drought-tolerant wheat genotypes. Based agronomic traits, water use efficie y and drought indices, BW141 X LM71, LM71 X BW162, BW140 X LM70, BW162 X BW140, BW141 X LM26, BW162 X LM71, BW152 X LM71, LM70 X BW141, LM75 X LM47 and LM70 X BW140 were selected and recommended for future breeding and crop production especially in the dryland agricultural systems.

Acknowledgements University of South Africa (UNISA), the African Centre of Crop Improvement (ACCI) of University of KwaZulu Natal (UKZN) and the Institut de Recherche pour le Dévelopement (IRD)/France are thanked for the overall research support. The research staff of the University of KwaZulu Natal's Ukulinga Research Farm are thanked for technical support.

Author contributions Maltase Mutanda, Hussein Shimelis, Vincent Chaplot, Kwame W Shamuyarira and Sandiswa Figlan wrote the main manuscript text. Maltase Mutanda, Hussein Shimelis and Sandiswa Figlan prepared all the tables. Maltase Mutanda and Kwame W Shamuyarira prepared the Fig. 1. All the authors reviewed the manuscript and agreed.

Funding Open access funding provided by University of South Africa. This study was based on generous financial support from the Water Research Commission of the Republic of South Africa (WRC Project No. C2020/2021-00646).

Data availability Data is provided within the manuscript and supplementary information fi es. The raw data fi es analyzed during the present study are available from the corresponding author upon a reasonable request.

Declarations

Ethics approval and consent to participate The parental genotypes used to were provided by International Maize and Wheat Improvement Centre (CYMMT), the wheat populations were developed following the local and national guidelines.

Consent for publication All the authors have given consent for publication of manuscript.

Competing interests The authors declare no competing interests.

References

1. Kumar P, Dheer V, Kumar P, Singh J, Singh KK, Kumar Y, Singh AK. Effect of irrigation scheduling and different sowing dates on growth and yield of wheat (*Triticum aestivum* L.). Int J Environ Clim Change. 2024;14:155–61. https://doi.org/10.9734/ijecc/2024/v14i13820.
2. Singh S, Kaur J, Ram H, Singh J, Kaur S. Agronomic bio-fortific tion of wheat (*Triticum aestivum* L.) to alleviate zinc deficien y in human being. Rev Environ Sci Biotechnol. 2023;22:505–26.
3. OlaOlorun BM, Shimelis HA, Mathew I. Variability and selection among mutant families of wheat for biomass allocation, yield and yield-related traits under drought-stressed and non-stressed conditions. J Agron Crop Sci. 2020;207:404–21. https://doi.org/10.1111/jac.12459.
4. van Dijk M, Morley T, Rau ML, Saghai Y. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. Nat Food. 2021;2:494–501. https://doi.org/10.1038/s43016-021-00322-9.
5. Tadesse W, Bishaw Z, Assefa S. Wheat production and breeding in Sub-Saharan Africa. Int J Clim Chang Strateg Manag. 2019;11:696–715.
6. Tadesse BZ, Assefa SW. Wheat production and breeding in Sub-Saharan Africa: challenges and opportunities in the face of climate change. Int J Clim Chang Strateg Manag. 2019;11:696–715.
7. Megersa O, Tadesse F, Ofga L, Legesse Z, Abro H. Large scale demonstration of irrigated wheat production technologies in bedeno district of eastern hararghe zone, oromia national regional state. Ethiopia Res Dev. 2023. https://doi.org/10.11648/j.rd.20230401.12.
8. Yildiz V, Hatipoglu MA, Kumcu Y. Water and wastewater management. Cham: Springer International Publishing; 2022.
9. Qiu W, Ma X, Cao H, Huang T, She X, Huang M, et al. Improving wheat yield by optimizing seeding and fertilizer rates based on precipitation in the summer fallow season in drylands of the Loess Plateau. Agric Water Manag. 2022;264: 107489. https://doi.org/10.1016/j.agwat.2022.107489.
10. Monneveux P, Jing R, Misra SC. Phenotyping for drought adaptation in wheat using physiological traits. Front Physiol. 2012;3:429.
11. Leakey ADB, Ferguson JN, Pignon CP, Wu A, Jin Z, Hammer GL, et al. Water use efficiency as a constraint and target for improving the resilience and productivity of C_3 and C_4 crops. Annu Rev Plant Biol. 2019;70:781–808. https://doi.org/10.1146/annurev-arplant-042817-040305.
12. Hussain T, Hussain N, Tahir M, Raina A, Ikram S, Maqbool S, et al. Impacts of drought stress on water use efficie y and grain productivity of rice and utilization of genotypic variability to combat climate change. Agronomy. 2022;12:2518. https://doi.org/10.3390/agronomy12102518.
13. Munjonji L, Ayisi KK, Vandewalle B, Dhau I, Boeckx P, Haesaert G. Yield performance, carbon assimilation and spectral response of triticale to water stress. Exp Agric. 2017;53:100–17.
14. Hu YC, Shao HB, Chu LY, Gang W. Relationship between water use efficie y (WUE) and production of different wheat genotypes at soil water defici . Colloids Surf B Biointerfaces. 2006;53:271–7.
15. Alotaibi M, El-Hendawy S, Mohammed N, Alsamin B, Refay Y. Appropriate application methods for salicylic acid and plant nutrients combinations to promote morpho-physiological traits, production, and water use efficie y of wheat under normal and deficit irrigation in an arid climate. Plants. 2023;12:1368.
16. Zhang X, Chen S, Sun H, Wang Y, Shao L. Water use efficiency and associated traits in winter wheat cultivars in the North China Plain. Agric Water Manag. 2010;97:1117–25.
17. Yong'an L, Quanwen D, Zhiguo C, Deyong Z. Effect of drought on water use efficie y, agronomic traits and yield of spring wheat landraces and modern varieties in Northwest China. Afr J Agric Res. 2010;5:1598–608.
18. Boutraa T, Akhkha A, Al-Shoaibi AA, Alhejeli AM. Effect of water stress on growth and water use efficie y (WUE) of some wheat cultivars (*Triticum durum*) grown in Saudi Arabia. J Taibah Univ Sci. 2010;3:39–48. https://doi.org/10.1016/s1658-3655(12)60019-3.
19. Mathew I, Shimelis H, Mutema M, Clulow A, Zengeni R, Mbava N, Chaplot V. Selection of wheat genotypes for biomass allocation to improve drought tolerance and carbon sequestration into soils. J Agron Crop Sci. 2019;205:385–400.

20. Shamuyarira KW, Shimelis H, Figlan S, Chaplot V. Combining ability analysis of yield and biomass allocation related traits in newly developed wheat populations. Sci Rep. 2023;13:11832.
21. Aycan M, Baslam M, Ozdemir B, Asiloglu R, Mitsui T, Yildiz M. Direct contribution of the maternal genotype on the transgenerational salinity tolerance in wheat (*Triticum aestivum* L.). Environ Exp Bot. 2021;192:104648. https://doi.org/10.1016/j.envexpbot.2021.104648.
22. Chimonyo VGP, Modi AT, Mabhaudhi T. Water use and productivity of a sorghum–cowpea–bottle gourd intercrop system. Agric Water Manag. 2016;165:82–96. https://doi.org/10.1016/j.agwat.2015.11.014.
23. Everson CS, Mengistu MG, Gush MB. A field assessment of the agronomic performance and water use of Jatropha curcas in South Africa. Biomass Bioenergy. 2013;59:59–69.
24. Jing W, Wu H, Gu H, Xiao Z, Wang W, Zhang W, et al. Response of grain yield and water use efficiency to irrigation regimes during midseason indica rice genotype improvement. Agriculture. 2022;12:1647.
25. Hussain T, Hussain N, Ahmed M, Nualsri C, Duangpan S. Impact of nitrogen application rates on upland rice performance, plant under varying sowing times. Sustainability. 2022. https://doi.org/10.3390/su14041997.
26. Rosielle AA, Hamblin J. Theoretical aspects of selection for yield in stress and non-stress environment[1]. Crop Sci. 1981;21:943–6. https://doi.org/10.2135/cropsci1981.0011183x002100060033x.
27. Fischer RA, Maurer R. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust J Agric Res. 1978;29:897. https://doi.org/10.1071/ar9780897.
28. Ramirez-Vallejo P, Kelly JD. Traits related to drought resistance in common bean. Euphytica. 1998;99:127–36.
29. Jafari A, Paknejad F, JAMI AM. Evaluation of selection indices for drought tolerance of corn (*Zea mays* L.) hybrids. 2009.
30. Fernandez GCJ. Effective selection criteria for assessing plant stress tolerance. 1993.
31. Gavuzzi P, Rizza F, Palumbo M, Campanile RG, Ricciardi GL, Borghi B. Evaluation of field and laboratory predictors of drought and heat tolerance in winter cereals. Can J Plant Sci. 1997;77:523–31. https://doi.org/10.4141/p96-130.
32. Bouslama M, Schapaugh WT. Stress tolerance in soybeans. I. evaluation of three screening techniques for heat and drought tolerance. Crop Sci. 1984. https://doi.org/10.2135/cropsci1984.0011183x002400050026x.
33. Payne Roger HR. A guide to multivariate analysis in Genstat® (18th ed.). VSN International. 2015.
34. Mwadzingeni L, Shimelis H, Rees DJG, Tsilo TJ. Genome-wide association analysis of agronomic traits in wheat under drought-stressed and non-stressed conditions. PLoS ONE. 2017;12:e0171692–e0171692.
35. Shamuyarira KW, Shimelis H, Tapera T, Tsilo TJ. Genetic advancement of newly developed wheat populations under drought-stressed and non-stressed conditions. J Crop Sci Biotechnol. 2019;22:169–76. https://doi.org/10.1007/s12892-018-0262-0.
36. Mwadzingeni L, Shimelis H, Tesfay S, Tsilo TJ. Screening of bread wheat genotypes for drought tolerance using phenotypic and proline analyses. Front Plant Sci. 2016;7:1276.
37. Semahegn Y, Shimelis H, Laing M, Mathew I. (2020) Evaluation of bread wheat (*Triticum aestivum* L.) genotypes for yield and related traits under drought stress conditions. Acta Agriculturae Scandinavica, Section B Soil Plant Sci. 2020;70:474–84. https://doi.org/10.1080/09064710.2020.1767802.
38. Dorostkar S, Dadkhodaie A, Heidari B. Evaluation of grain yield indices in hexaploid wheat genotypes in response to drought stress. Arch Agron Soil Sci. 2014;61:397–413. https://doi.org/10.1080/03650340.2014.936855.
39. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. Plant drought stress: effects, mechanisms and management. Agron Sustain Dev. 2009;29:185–212. https://doi.org/10.1051/agro:2008021.
40. Gui YW, Sheteiwy MS, Zhu SG, Batool A, Xiong YC. Differentiate effects of non-hydraulic and hydraulic root signaling on yield and water use efficiency in diploid and tetraploid wheat under drought stress. Environ Exp Bot. 2021. https://doi.org/10.1016/j.envexpbot.2020.104287.
41. Guasconi D, Manzoni S, Hugelius G. Climate-dependent responses of root and shoot biomass to drought duration and intensity in grasslands–a meta-analysis. Sci Total Environ. 2023;903: 166209. https://doi.org/10.1016/j.scitotenv.2023.166209.
42. Anwaar HA, Perveen R, Mansha MZ, Abid M, Sarwar ZM, Aatif HM, et al. Assessment of grain yield indices in response to drought stress in wheat (*Triticum aestivum* L.). Saudi J Biol Sci. 2020;27:1818–23.
43. Meena SL, Sparkes DL. Resource use efficiency of different wheat species under drought stress. Indian J Agric Sci. 2018;88:1349–53.
44. Mansour E, Abdul-Hamid MI, Yasin MT, Qabil N, Attia A. Identifying drought-tolerant genotypes of barley and their responses to various irrigation levels in a Mediterranean environment. Agric Water Manag. 2017;194:58–67. https://doi.org/10.1016/j.agwat.2017.08.021.
45. Attia A, Rajan N, Nair SS, DeLaune PB, Xue Q, Ibrahim AMH, et al. Modeling cotton lint yield and water use efficiency responses to https://doi.org/10.2134/agronj2015.0437
46. Sánchez-Reinoso AD, Ligarreto-Moreno GA, Restrepo-Díaz H. Evaluation of drought indices to identify tolerant genotypes in common bean bush (*Phaseolus vulgaris* L.). J Integr Agric. 2020;19:99–107. https://doi.org/10.1016/s2095-3119(19)62620-1.
47. Mohammadi M, Sharifi P, Karimizadeh R, Shefazadeh MK. Relationships between grain yield and yield components in bread wheat under different water availability (dryland and supplemental irrigation conditions). Not Bot Horti Agrobot Cluj Napoca. 2012;40:195. https://doi.org/10.15835/nbha4017350.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.