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Genetic variability and trait associations in bread wheat (*Triticum aestivum* L.) genotypes under drought-stressed and well-watered conditions

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Abstract

Drought is one of the most important yield-limiting abiotic stresses threatening wheat production and productivity. Development of wheat genotypes with enhanced grain yield under drought-stressed conditions depend on the extent of genetic variation present for drought tolerance-related traits. This study was carried out to determine the level of genetic variation and associations of yield and yield attributing traits among 196 bread wheat genotypes under drought-stressed and well-watered conditions. The genotypes were evaluated under greenhouse and field conditions and phenotyped for yield and yield-related traits. The genotypes varied significantly for the traits under both conditions. Grain yield ranged from 2.13 to 3.74 t ha⁻¹ and from 2.52 to 5.06 t ha⁻¹ under drought-stressed and well-watered conditions, respectively. Under both conditions, variances due to genotype were higher than environment and genotype × environment interaction variances for all the traits. Estimates of phenotypic coefficient of variation (PCV) were higher than genotypic coefficient of variation (GCV) for all the traits under both conditions, with both PCV and GCV being highest for kernel weight spike⁻¹ and lowest for spike fertility. Under both conditions, broad-sense heritability estimates ranged from moderately high to very high, accompanied with high genetic advance as a percentage of the mean. Fertile spikelets spike⁻¹, one thousand kernel weight, kernel weight spike⁻¹, biomass yield and harvest index manifested high positive genotypic and phenotypic correlations and positive direct effects on grain yield under both conditions. The first five principal components accounted for 78.4% (well-watered) and 76.0% (drought-stressed) of the variation among the genotypes. The 196 genotypes were delineated into six major clusters under both water conditions, with clusters 3 (well-watered) and cluster 5 (drought-stressed) containing genotypes with the highest ability to tolerate drought stress. Genotypes Alidoro, Bolo, Dinknesh, ETBW8491 and ETBW172938 had high stable yields under both conditions. The identified traits and genotypes were drought tolerant and could be exploited to develop novel genotypes for drought stress tolerance.

Keywords Broad-sense heritability, Drought stress, Genotypic correlation, Principal component analysis, Variance components

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Introduction

Bread wheat (*Triticum aestivum* L., $2n=6x=42$, AABBDD) is the most extensively grown cereal staple food crop for driving global food security and economy (Bapela et al. 2022). In Ethiopia, wheat plays a crucial role in the social and economic life of the people and it is consumed in a variety of forms such as local bread, porridge (genfo), local beer (tela), roasted grain (kolo), boiled grain (nifro), pasta, macaroni, and different confectionary products (Tadesse et al. 2019; Alemu et al. 2020). However, the production and productivity of wheat in Ethiopia is limited by adverse climatic conditions, prominent among which is the incidence of drought (Belay et al. 2017; Senbeta and Worku 2023). The limitation imposed by the incidence of drought is further aggravated by global climate change, as well as the semi-arid to arid nature of the major wheat producing farming regions of Ethiopia.

Drought stress negatively impacts wheat growth and productivity at all stages of development. However, its effects are more pronounced when the stress occurred at heading, anthesis and grain filling (Khadka et al. 2020 and Zhang et al. 2018). Occurrence of drought stress during periods surrounding anthesis and grain filling stages leads to a reduction in nutrient uptake and photosynthetic efficiency, abortion of ovules, reduction in number of grains per spike, production of shrunken kernels, reduction in grain weight and finally, loss in grain yield (Pradhan et al. 2012; Iqbal 2019; Bapela et al. 2022). In general, conditions of drought stress retards plant growth, development and yield by altering the inherent relationships among grain yield and its component traits (Afzal et al. 2017). In wheat, grain yield reduction due to drought stress could be as high as 65% (Bennett et al. 2012).

Options available to reduce the effects of drought stress on crop plants include the use of irrigation and drought resistant varieties. In Ethiopia, application of supplementary irrigation water is neither sustainable nor readily available to resource-constrained farmers, particularly in the major wheat growing regions of the country. However, the development and adoption of drought resilient and high yielding genotypes is a highly sustainable and effective way of addressing the limitations imposed by drought stress on the production and productivity of wheat, and is compatible with other stress management strategies. It is therefore imperative to develop and adopt genotypes with broad genetic base, and wide adaptability and resilience to changes in climatic factors, while maintaining high yields under non-stressed and stressed conditions (Bapela et al. 2022; Pandey et al. 2022).

Selection for agronomic traits through the conventional crop breeding techniques has considerably improved wheat productivity under both well-watered

and drought-stressed conditions. Grain yield of wheat is directly affected by environment and yield contributing traits (Mathew et al. 2018 and Mwadzingeni et al. 2017) such as number of tillers plant⁻¹, number spikelets spike⁻¹, fertile spikelets spike⁻¹, number of kernels spike⁻¹, spike fertility, kernels weight spike⁻¹ and thousand kernels weight. Other yield-related traits such as days to heading, grain filling period, days to maturity, plant height, spike length, flag leaf area, above ground biomass yield and harvest index indirectly affect yield by exerting their influence on yield-component traits (Tshikunde et al. 2019; Yadav et al. 2021).

In order to improve wheat for tolerance to drought, information is required on nature and extent of available genetic variability for the trait (Singh et al. 2020). Such information would help the plant breeder to decide on appropriate breeding strategies necessary to facilitate progress in selection for drought tolerance. The influence of drought stress on crop performance vary with genotype, environment and genotype by environment interaction (Hoffman et al. 2009). Semahegn et al. (2020) indicated the occurrence of significant genetic variation for yield and yield component traits in bread wheat genotypes evaluated under drought-stressed and non-stressed conditions. However, there is a need to investigate the genetic basis of such variations and the nature of association among yield and yield-related traits under drought-stressed and well-watered conditions in order to select promising genotypes for drought tolerance improvement. Understanding the nature of associations among traits require such tools as path coefficient analysis, which partitions the correlation coefficients into components of direct and indirect influential effects. This helps to simplify selection of complex traits such as drought tolerance in wheat populations (Shamuyarira et al. 2019b). Therefore, this investigation was conducted to estimate the magnitude of genetic variability for drought tolerance among 196 bread wheat genotypes and assess the associations among yield and its component traits under drought-stressed and well-watered conditions.

Materials and methods

Study site, experimental materials and data collection

The field and greenhouse experiments were carried out at Crop Research Field of Wachemo University, Hosanna, Ethiopia during the 2020–2021 and 2021–2022 cropping seasons. The Kulumsa Agricultural Research Center (KARC) provided 196 genotypes of bread wheat. One hundred ninety six bread wheat genotypes sourced from the Ethiopian Institute of Agricultural Research, were used for the study. The genotypes were assessed in both well-watered and drought-stressed conditions. A total of 196 bread wheat genotypes sourced from the

Table 1 Mean squares and significant test analysis of variance for 16 agronomic traits of 196 bread wheat genotypes evaluated under well-watered and drought-stressed conditions

Sources		Well-watered conditions															
DF	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMV	HI	KWS	TKW	GY	
G	195	199**	71.2**	131.0**	536.3**	19.8**	6.1**	173.5**	11.9**	38.5**	148.3**	14.9**	5.3**	41.7**	1.5**	149.9**	1.3**
E	3	2981**	1106.3**	4828**	4205.1**	1853.6**	77.3**	1898.3**	1344.7**	1928.3**	7527.7**	926.4**	66.2**	4519.7**	6.5**	1433.8**	16.3**
G×E	585	19.8**	30.6**	19.9 ns	136.2**	10.8**	1.7**	76.2**	5.5 ns	32.1 ns	61.3**	8.00 ns	1.5**	25.0 ns	0.5**	51.7**	0.4 ns
Residuals	784	4.74	10.69	17.7	23.1	3.92	0.175	17.11	6.05	31.43	43.9	7.97	0.847	27	0.05	6.74	0.278
CV (%)		6.01	7.16	4.51	8.28	12.38	6.24	8.04	6.88	8.65	6.11	2.56	5.97	8.37	6.06	5.12	11.05
Sources		Drought-stressed conditions															
DF	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMV	HI	KWS	TKW	GY	
G	195	165.9**	52.6**	105.1**	290.2**	1.49 ns	2.6**	119.0**	5.72**	5.753**	58.2**	3.02 ns	3.624	22.1 ns	1.3**	123.4**	0.74**
E	3	3700.7**	3103**	9679**	2284.9**	526.7**	42.4**	9452.6**	495.8**	282.986**	835.9**	457.6**	33.269	3963.6**	3.9**	4199.3**	21.1**
G×E	585	22.4**	30.9**	22.5**	108.2**	1.5 ns	1.28**	79.6**	3.82**	3.778**	37.4**	2.2 ns	1.266	17.7 ns	0.42**	36**	0.25**
Residuals	784	3.4	20.16	10.5	76.4	3.09	0.43	20.1	1.07	1.048	13.68	4.61	0.348	24.8	0.0778	7.6	0.0532
CV (%)		6.52	9.11	5.03	9.49	11.54	8.55	10.38	7.02	6.71	5.93	2.04	6.85	9.06	7.21	6.43	10.84

ns non-significant, *DH* Days to heading, *GFP* Grain filling period (days), *DM* Days to maturity, *PH* Plant height (cm), *NTPP* Number of tillers plant⁻¹, *SL* Spike length (cm), *FLA* Flag leaf area (cm²), *SPS* Spikelets spike⁻¹, *FSPS* Fertile spikelets spike⁻¹, *NKPS* Number of kernels spike⁻¹, *SF* Spike fertility (%), *BMV* Biomass yield (t ha⁻¹), *HI* Harvest index (%), *KWS* Thousand kernels weight (g), *TKW* Thousand kernels weight (g), and *GY* Grain yield (t ha⁻¹)
G Genotypes, *E* Environments, *G × E* Genotype by environment interactions, *CV* (%) Coefficient of variation in percent
 **Highly significant, *significant

Table 2 Mean squares from combined analysis of variance of 16 agronomic traits of bread wheat evaluated in four environments under well-watered and drought-stressed conditions

Sources	DF	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
G	195	340.8**	216**	443.6**	442.14**	27.24**	48.8**	485.7**	76.19**	200.9**	208.64**	307.6**	25.24**	406.96**	3.53**	486.3**	5.70**
W	1	214.4**	1356**	465**	107,209**	4583**	1420**	5395**	13,710**	15,017**	132,107**	5975**	1093**	36,651**	357**	35,844**	1001**
E	3	5004**	6913**	18,907**	29,784**	3003**	156.4**	10,032**	2368**	2013**	9787**	427**	274**	11,835**	11.3**	4703**	53.4**
G×W	195	11.5**	15.52**	8.49 ^{ns}	38.45**	8.61**	1.36**	30.27 ^{ns}	3.21 ^{ns}	4.25*	43.09**	5.73 ^{ns}	0.60 ^{ns}	12.9 ^{ns}	0.12 ^{ns}	8.99 ^{ns}	0.12 ^{ns}
G×E	585	12.1**	20.31**	9.86 ^{ns}	47.50**	2.20 ^{ns}	0.45 ^{ns}	30.34 ^{ns}	2.87 ^{ns}	3.24 ^{ns}	31.59 ^{ns}	4.92 ^{ns}	0.41 ^{ns}	16.6 ^{ns}	0.09 ^{ns}	17.37 ^{ns}	0.13 ^{ns}
W×E	3	810.7**	1144**	910**	6227.5**	299**	67.71**	3785**	746**	776**	4508.2**	1109**	53.05**	4285**	14.2**	676**	32.9**
G×W×E	585	14.82**	17.41**	12.55**	24.94 ^{ns}	2.73 ^{ns}	0.83**	9.82*	2.35 ^{ns}	1.75 ^{ns}	28.73 ^{ns}	5.01 ^{ns}	0.94*	10.9 ^{ns}	8.38*	20.91**	0.36 ^{ns}
Error	1568	14.26	17.76	12.71	43.58	3.46	3.52	53.13	7.23	11.34	12.60	4.87	1.84	16.3	0.89	27.7	0.52
Mean		63.00	55.85	117.62	87.29	5.02	8.68	35.17	22.60	20.12	61.81	89.23	9.44	34.4	2.49	39.7	3.62
CV (%)		5.12	7.63	2.85	9.57	36.07	10.56	20.44	7.41	9.08	9.20	2.48	10.77	11.7	21.4	13.2	15.2

^{ns} non-significant, ^{DH} Days to heading, ^{GFP} Grain filling period (days), ^{DM} Days to maturity, ^{PH} Plant height (cm), ^{NTPP} Number of tillers plant⁻¹, ^{SL} Spike length (cm), ^{FLA} Flag leaf area (cm²), ^{SPS} Spikelets spike⁻¹, ^{FSPS} Fertile spikelets spike⁻¹, ^{NKPS} Number of kernels spike⁻¹, ^{SF} Spike fertility (%), ^{BMY} Biomass yield (t ha⁻¹), ^{HI} Harvest index (%), ^{KWS} Kernels weight spike⁻¹ (g), ^{TKW} Thousand kernels weight (g), and ^{GY} Grain yield (t ha⁻¹)
 G Genotypes, W Water regimes, E Environments, G × W Genotype by Water regimes interactions, G × E Genotype by environment interactions, W × E Water regimes by Environment interactions, G × W × E Genotype by Water regimes by Environment interactions

**Highly significant, *significant

Table 3 Minimum, maximum, and mean values of agronomic traits under well-watered conditions

Traits	Minimum		Maximum		Mean
	Value	Genotype	Value	Genotype	
Days to heading	54.50	ETBW8311	79.63	Digelu	62.81
Grain filling period (days)	46.88	Menze	63.00	ETBW172864	55.29
Days to maturity	109.20	ETBW9441	132.12	ET13A2	118.08
Plant height (cm)	70.00	ETBW8984	132.00	ETBW172955	93.45
Number of tillers plant ⁻¹	3.25	ETBW9179	10.88	ETBW9202	6.75
Spike length (cm)	7.56	WANE	12.13	Biqa	9.32
Flag leaf area (cm ²)	26.72	ETBW8751	50.19	ETBW9135	36.93
Spikelets spike ⁻¹	21.66	ETBW9441	30.60	ETBW172938	24.76
Fertile spikelets spike ⁻¹	18.65	ETBW9441	28.60	ETBW172938	22.37
Number of kernels spike ⁻¹	57.00	ETBW9441	85.80	ETBW172938	68.67
Spike fertility (%)	86.10	ETBW9441	93.46	ETBW172938	90.16
Biomass yield (t ha ⁻¹)	8.22	ETBW172862	12.54	Alidoro	10.05
Harvest index (%)	31.42	ETBW8987	43.75	Bolo	37.39
Kernel weight spike ⁻¹ (g)	1.75	ETBW9435	4.45	ETBW172938	2.83
One thousand kernel weight (g)	30.32	ETBW9441	58.62	Alidoro	43.03
Grain yield (t ha ⁻¹)	2.52	Menze	5.06	Alidoro	3.76

Ethiopian Institute of Agricultural Research, were used for the study. The genotypes were selected based on their yield performance at national yield trials under drought-stressed condition. The materials are comprised of 48 released bread wheat varieties and 148 advanced bread wheat genotypes/lines. These advanced lines are introduced from CIMMYT, ICARDA and generated from local crosses. The list of the 196 bread wheat genotypes used in the study is presented in S2. The pH of the soil made of clay loam in the research site was 6.81. One hundred eighty eight testing and eight check genotypes were planted in a 14×14 lattice design with two replications. All agronomic practices were kept optimum for all lines and check varieties. Data on the yield and yield-related traits such as number of days to heading (DH), days to maturity (DM), grain filling period (GFP), number of tillers plant⁻¹ (NTPP), plant height (PH), flag leaf area (FLA), spike length (SL), number of spikelets spike⁻¹ (SPS), number of kernels spike⁻¹ (NKPS), fertile spikelets spike⁻¹ (FSPS), biomass yield (BMY), kernels weight spike⁻¹ (KWS), 1000 kernel weight (TKW), grain yield (GY), harvest index (HI), and spike fertility (SF) were considered for this study.

Data statistical analyses

The data was analysed using a combined analysis of variance, using the general linear model (GLM) procedure in SAS version 9.3 (SAS Institute, 2004), after checking for homogeneity of variance. The analysis was done

separately for each water regime and then combined. Genotypic and phenotypic correlations as well as path coefficient analysis were calculated as per Popat and Banakara (2020) by R software using variability package. Statistical significance among treatment means was determined using the Least Significant Difference (LSD) at $p < 0.01$ and $p < 0.05$ levels. Negative variances were adjusted to zero (Borojevic 1990; Johnson et al. 1955). The heritability in broad sense (H^2B) estimates were calculated from the phenotypic variance (σ^2p) and the genotypic variance (σ^2g) according to Allard (1999) as:

$$H^2B = \frac{\sigma^2g}{(\sigma^2g + \sigma^2gwls / wls + \sigma^2gls / ls + \sigma^2glw / lw + \sigma^2gsw / sw + \sigma^2gs / s + \sigma^2gw / w + \sigma^2gl / l + \sigma^2e / rls) + \sigma^2g} = \frac{\sigma^2g}{(\sigma^2g + \sigma^2gxe / e + \sigma^2e / re) + \sigma^2g} = \frac{\sigma^2g}{\sigma^2p}$$

Where σ^2e = environmental variance, σ^2g = genotypic variance, σ^2gl = genotype by site interaction variance, σ^2gs = genotype by season interaction variance, σ^2gw = genotype by water regime interaction variance, σ^2gls = genotype by site by season interaction variance, σ^2glw = genotype by site by water regime interaction; σ^2gws = genotype by water regime by site interaction variance, σ^2gws = genotype by site by water regime by season interaction, r = replication.

Results and discussion

Effect of genotypes, water regimes and testing environments on trait variability

The results from separate and combined analysis of variance revealed significant differences among the studied bread wheat genotypes for all the 16 agronomic traits

Table 4 Minimum, maximum, and mean values of agronomic traits under drought-stressed conditions

Traits	Minimum		Maximum		Mean
	Value	Genotype	Value	Genotype	
Days to heading	56.00	ETBW8311	78.00	ET-13A2	63.19
Grain filling period (days)	49.88	Menze	63.88	ETBW8676	56.42
Days to maturity	110.88	ETBW172864	131.88	Digelu	119.61
Plant height (cm)	58.97	ETBW9413	89.35	ETBW8862	72.39
Number of tillers plant ⁻¹	2.00	ETBW9412	6.81	ETBW9202	3.57
Spike length (cm)	6.45	Menze	9.66	Biqa	7.70
Flag leaf area (cm ²)	21.78	ETBW9091	40.54	ETBW172936	30.00
Spikelets spike ⁻¹	19.84	Honqolo	25.17	ETBW172938	21.94
Fertile spikelets spike ⁻¹	17.44	Honqolo	22.98	ETBW172938	19.64
Number of kernels spike ⁻¹	53.77	ETBW9441	70.75	ETBW172938	60.78
Spike fertility (%)	87.48	ETBW172864	91.34	ETBW 9137	89.23
Biomass yield (t ha ⁻¹)	6.61	Menze	9.66	ETBW 8491	7.95
Harvest index (%)	29.38	ETBW8987	40.01	Bolo	33.65
Kernel weight spike ⁻¹ (g)	1.28	ETBW 8944	3.43	Dinknesh	2.46
One thousand kernel weight (g)	19.05	ETBW 9441	42.38	Dinknesh	33.88
Grain yield (t ha ⁻¹)	2.13	Doddota	3.74	Bolo	2.70

under drought-stressed and well-watered conditions. In separate analysis of variance, highly significant genotypic differences (≤ 0.001) were found for all the traits under both water regimes (Table 1). In the combined analysis of variance, highly significant ($p < 0.01$) effects of genotypes, environments and water regimes were

obtained for all the studied traits, indicating the presence of a wide genetic variability that could be exploited for wheat improvement (Table 2). The interaction effect of genotype \times water regime on days to heading, grain filling period, plant height number of tillers per plant, spike length and number of kernels spike were highly

Table 5 Estimates of variance components, broad sense heritability, genetic advance and genetic advance as percent of mean for 16 agronomic traits in 196 bread wheat genotypes under well-watered conditions

Traits	σ^2_e	σ^2_g	σ^2_p	GCV	ECV	PCV	H ² B (%)	GA	GAM (%)
Days to heading	34.28	172.0	218.4	20.91	9.33	22.90	83.37	24.70	39.38
Grain filling period	32.46	137.2	179.5	21.19	10.30	23.58	80.71	21.71	39.26
Days to maturity	75.32	453.3	543.8	18.04	7.35	19.49	85.74	40.67	34.47
Plant height (cm)	70.85	336.6	437.11	19.70	9.04	21.68	82.60	34.40	36.94
Number of tillers plant ⁻¹	0.79	1.32	2.52	22.53	17.43	28.48	62.56	1.87	36.76
Spike length (cm)	1.08	7.89	10.8	30.03	11.11	32.03	87.96	5.43	58.13
Flag leaf area (cm ²)	32.53	117.0	165.73	29.25	15.42	33.06	78.26	19.74	53.38
Spikelets spike ⁻¹	13.91	34.73	52.84	23.87	15.11	28.25	71.40	10.27	41.61
Fertile spikelets spike ⁻¹ (%)	10.24	22.73	34.25	21.38	14.35	25.75	68.94	8.17	36.62
Number of kernels spike ⁻¹	12.09	93.12	114.75	14.10	5.08	14.97	88.52	18.73	27.34
Spike fertility (%)	15.34	117.0	143.46	12.00	4.35	12.77	88.37	20.98	23.27
Biomass yield (t ha ⁻¹)	2.02	8.35	11.56	28.72	14.13	32.01	80.52	5.35	53.17
Harvest index (%)	5.58	59.92	70.1	20.62	6.29	21.55	91.48	15.27	40.68
Kernels weight spike ⁻¹ (g)	0.49	1.52	2.48	43.49	24.73	50.10	75.62	2.21	78.16
Thousand kernels weight (g)	26.83	134.3	192.6	26.9	12.02	30.92	75.70	20.80	48.29
Grain yield (t ha ⁻¹)	0.37	1.46	2.36	32.05	16.13	35.88	79.78	2.23	59.06

σ^2_e environment variance, σ^2_g genotype variance, σ^2_p phenotype variance, ECV Environment coefficient of variation PCV Phenotypic coefficient of variation, GCV genotypic coefficient of variation, H²B broad sense heritability, GA genetic advance, GAM genetic advance as percent of mean

Table 6 Estimates of variance components, broad sense heritability, genetic advance and genetic advance as percent of mean for 16 agronomic traits in 196 bread wheat genotypes under drought-stressed conditions

Traits	σ^2_e	σ^2_g	σ^2_p	GCV	ECV	PCV	H ² B (%)	GA	GAM (%)
Days to heading	19.05	170.3	217.5	20.63	6.90	23.34	89.94	25.53	40.37
Grain filling period	24.89	113.8	156.25	19.77	9.24	22.16	82.06	19.94	36.94
Days to maturity	36.22	434.4	510.2	17.78	5.13	18.88	92.30	41.31	35.24
Plant height (cm)	21.63	353.8	411.6	23.10	5.71	28.03	94.24	37.67	46.26
Number of tillers plant ⁻¹	0.88	0.91	2.05	25.03	24.69	40.11	50.70	1.40	36.77
Spike length (cm)	1.92	3.67	6.8	24.14	17.47	33.87	65.62	3.20	40.34
Flag leaf area (cm ²)	39.86	89.90	132.8	27.59	18.37	40.55	69.28	16.28	47.38
Spikelets spike ⁻¹	6.78	32.86	42.6	27.95	12.70	29.75	82.90	10.77	52.50
Fertile spikelets spike ⁻¹ (%)	4.63	21.87	29.01	26.08	12.00	27.42	82.53	8.76	48.87
Number of kernels spike ⁻¹	9.43	72.67	92.06	15.35	5.53	15.79	88.51	16.54	29.80
Spike fertility (%)	14.39	106.1	136.8	11.79	4.34	14.49	88.06	19.94	22.82
Biomass yield (t ha ⁻¹)	1.87	5.88	8.92	27.48	15.50	37.57	75.86	4.36	49.38
Harvest index (%)	5.42	57.80	74.3	24.61	7.54	25.62	91.43	15.00	48.55
Kernels weight spike ⁻¹ (g)	0.36	0.94	1.65	44.89	27.78	52.22	72.31	1.70	78.74
Thousand kernels weight (g)	13.52	105.2	135.5	28.23	10.12	34.36	88.61	19.91	54.83
Grain yield (t ha ⁻¹)	0.18	0.85	1.55	34.82	16.07	37.84	82.44	1.72	65.22

σ^2_e Error mean square, σ^2_g genotype variance, σ^2_p phenotype variance, ECV Environment coefficient of variation PCV Phenotypic coefficient of variation, GCV genotypic coefficient of variation, H²B broad sense heritability, GA genetic advance, GAM genetic advance as percent of mea

significant. Genotype \times environment interaction effect was highly significant for days to heading, grain filling period and plant height. For all the traits, effects of water regime \times environment interaction was highly significant ($p < 0.01$). The three-way interaction effect of genotype, water regime and environment was significant only for days to heading, grain filling period, days to maturity, spike length, thousand kernels weight, flag leaf area, biomass yield and kernels weight spike⁻¹. The existence of genetic variability among the studied genotypes for traits related to drought tolerance is important for successful breeding aimed at developing genotypes tolerant to stress environments (Mathew et al. 2018; Mwadingeni et al. 2017; Semahegn et al. 2021).

Genotypic response of agronomic traits

Days to heading, days to maturity and grain filling periods

The minimum, maximum, and mean performance of genotypes for agronomic traits grown under well-watered and drought-stressed conditions are presented in Tables 3 and 4. Under well-watered condition, days to heading (DH) ranged from 54.50 to 79.63 days with a mean of 62.81 days. Genotypes ETBW8311, ETBW9383, ETBW9411, ETBW8881, ETBW8676, and ETBW172864 (DH \leq 56.00 days) were considered to be early heading, while genotypes Digelu, ET13A2, ETBW9027, Menze, Dashen and Huluka (DH \geq 74.38 days) were late heading. Days to maturity (DM) was in the range of 109.2 to 132.12 days with a mean of 118.08 days. Genotypes

ETBW8944, ETBW9091 and ETBW9441 were the earliest maturing (DM \leq 109.88 days), while ET13A2, Digelu, ETBW172936 and ETBW9027 were the latest to mature (DM \geq 130.38 days). Grain filling period (GFP) was most lengthy for the genotypes ETBW8676 (62.63 days), ETBW8311 (62.13 days), Mitike (61.87 days) and Dure (61.75 days), and shortest for genotypes Laketch (48.13 days) and Menze (46.88 days).

Under drought-stressed conditions, DH ranged from 56.00 to 78.00 days with a mean of 63.24 days. Genotypes ETBW 9435, ETBW 9409, ETBW 9383, ETBW 8676, ETBW172996 and ETBW 8311 with DH \leq 57.00 days were early heading, whereas ET-13A2, Menze, ETBW 9027, Bolo, Galema and Meraro with DH \geq 74.13 days were the latest to heading. The earliest maturing genotypes (ETBW9091, ETBW9441 and ETBW172864) had DM \leq 112.00, while genotypes Digelu, ET-13A2, ETBW9027 and Galema with DM \geq 131.50 days were the latest maturing. Genotypes ETBW 8676 (63.88 days) and ETBW 8311 (62.00 days) had the longest GFP, while genotypes Hoggana (51.13 days) and Menze (49.88 days) had the shortest.

Consistent with the results of this study, Bayisa et al. (2019), as well as Olbana et al. (2021) had earlier shown that wheat genotypes could differ for DH, DM and GFP. Drought stress significantly increased number of days to heading and maturity and reduced grain filling period in bread wheat (Lemma et al. 2021). However, early heading and maturity are essential traits for improving

Table 7 Genotypic (above the diagonal) and phenotypic (below the diagonal) correlation coefficients for sixteen agronomic traits of 196 bread wheat genotypes evaluated under well-watered condition

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMV	HI	KWS	TKW	GY
DH	1															
GFP	-0.57**	1														
DM	0.82**	-0.04 ^{ns}	1													
PH	-0.17*	0.21*	0.06 ^{ns}	1												
NTPP	0.063 ^{ns}	0.19*	0.07 ^{ns}	0.11 ^{ns}	1											
SL	0.28**	0.21**	0.26**	0.19*	0.06 ^{ns}	1										
FLA	0.16*	0.087	0.04 ^{ns}	-0.18*	-0.04 ^{ns}	0.08 ^{ns}	1									
SPS	0.22**	0.28**	0.22**	0.15*	0.14*	0.15*	0.19*	1								
FSPS	0.20**	0.31**	0.27**	0.16*	0.15*	0.16*	0.16*	0.99**	1							
NKPS	0.34**	0.26**	0.32**	0.14*	0.15*	0.13 ^{ns}	0.16*	0.97**	0.98**	1						
SF	0.27**	0.38**	0.31**	0.17*	0.23**	0.08 ^{ns}	-0.04 ^{ns}	0.62**	0.72**	0.75**	1					
BMV	0.38**	0.44**	0.23**	0.21*	0.20*	0.14*	0.00 ^{ns}	0.65**	0.67**	0.66**	0.57**	1				
HI	0.19*	0.21**	0.15*	0.07 ^{ns}	0.00 ^{ns}	0.03 ^{ns}	0.13 ^{ns}	0.22*	0.22*	0.23**	0.18*	0.18*	1			
KWS	0.25**	0.42**	0.24**	0.26**	0.16*	0.14*	0.20**	0.71**	0.75**	0.70**	0.49**	0.82**	0.39**	1		
TKW	32**	0.29**	0.25**	0.37**	0.19*	0.12 ^{ns}	0.25**	0.56**	0.58**	0.55**	0.46**	0.84**	0.44**	0.90**	1	
GY	0.23**	0.35**	0.24**	0.22**	0.08 ^{ns}	0.13 ^{ns}	0.13 ^{ns}	0.61**	0.68**	0.57**	0.69**	0.89**	0.63**	0.84**	0.88**	1

^{ns} non-significant, *DH* Days to heading, *GFP* Grain filling period (days), *DM* Days to maturity, *PH* Plant height (cm), *NTPP* Number of tillers plant⁻¹, *SL* Spike length (cm), *FLA* Flag leaf area (cm²), *SPS* Spikelets spike⁻¹, *FSPS* Fertile spikelets spike⁻¹, *NKPS* Number of kernels spike⁻¹, *SF* Spike fertility (%), *BMV* Biomass yield (t ha⁻¹), *HI* Harvest index (%), *KWS* Kernels weight spike⁻¹(g), *TKW* Thousand kernels weight (g), and *GY* Grain yield (t ha⁻¹)

**Highly significant, *significant

Bold indicate the diagonal that separate genotypic correlation from phenotypic correlation coefficients under well-watered conditions

Table 8 Genotypic (above the diagonal) and phenotypic (below the diagonal) correlation coefficients for sixteen agronomic traits of 196 bread wheat genotypes evaluated under drought-stressed condition

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
DH	1	0.016 ^{ns}	0.88**	0.026 ^{ns}	-0.01 ^{ns}	-0.067 ^{ns}	0.151*	-0.158*	-0.20**	-0.027 ^{ns}	0.124 ^{ns}	-0.056 ^{ns}	0.612**	0.045 ^{ns}	0.56 ^{ns}	0.248**
GFP	-0.22**	1	0.169*	-0.233 ^{ns}	0.288**	-0.85**	0.311**	0.392**	0.542**	0.82**	-0.062 ^{ns}	0.85**	-0.11 ^{ns}	0.265**	0.293**	0.853**
DM	0.744**	0.49**	1	-0.01 ^{ns}	0.043 ^{ns}	-0.20**	0.407**	0.058 ^{ns}	0.041 ^{ns}	0.252*	-0.168 ^{ns}	0.075 ^{ns}	0.587**	0.238**	0.10 ^{ns}	0.375**
PH	-0.055 ^{ns}	0.014 ^{ns}	-0.04 ^{ns}	1	-0.045 ^{ns}	0.26**	0.234**	0.472**	0.476**	0.04 ^{ns}	0.007 ^{ns}	0.294**	-0.51**	0.125 ^{ns}	0.289**	0.034 ^{ns}
NTPP	-0.005 ^{ns}	0.103*	0.066 ^{ns}	0.063 ^{ns}	1	0.52**	-0.39**	0.974**	0.962**	0.403**	0.269**	0.52**	-0.17**	0.657**	0.534**	0.097 ^{ns}
SL	-0.068 ^{ns}	0.075 ^{ns}	-0.01 ^{ns}	0.173**	0.158**	1	0.084 ^{ns}	0.137 ^{ns}	0.166*	-0.24**	0.138*	0.088 ^{ns}	0.067 ^{ns}	-0.044 ^{ns}	-0.067 ^{ns}	0.09 ^{ns}
FLA	0.06 ^{ns}	0.048 ^{ns}	0.086 ^{ns}	-0.01 ^{ns}	0.058 ^{ns}	0.026 ^{ns}	1	0.274**	0.208**	0.083 ^{ns}	-0.191 ^{ns}	0.004 ^{ns}	-0.26**	0.169**	-0.167 ^{ns}	0.192**
SPS	0.025 ^{ns}	-0.006 ^{ns}	0.018 ^{ns}	0.031 ^{ns}	0.074 ^{ns}	-0.01 ^{ns}	0.05 ^{ns}	1	0.901**	0.920**	0.152*	0.624**	0.283**	0.247**	0.686**	0.715**
FSPS	0.022 ^{ns}	-0.007 ^{ns}	0.015 ^{ns}	0.033 ^{ns}	0.089 ^{ns}	-0.008 ^{ns}	0.044 ^{ns}	0.988**	1	0.981**	0.387**	0.712**	0.223**	0.722**	0.764**	0.769**
NKPS	0.04 ^{ns}	-0.048 ^{ns}	0.003 ^{ns}	0.006 ^{ns}	0.054 ^{ns}	-0.03 ^{ns}	0.091 ^{ns}	0.783**	0.793**	1	0.548**	0.433**	0.876**	0.763**	0.812**	0.874**
SF	-0.004 ^{ns}	-0.01 ^{ns}	-0.01 ^{ns}	0.039 ^{ns}	0.121*	-0.002 ^{ns}	0.006 ^{ns}	0.664**	0.772**	0.61**	1	0.317**	-0.043 ^{ns}	-0.059 ^{ns}	0.363 ^{ns}	0.401**
BMY	-0.059 ^{ns}	0.18**	0.07 ^{ns}	0.107*	0.105*	0.15**	0.11*	0.29**	0.303**	0.238**	0.264**	1	-0.081 ^{ns}	0.353**	0.904**	0.842**
HI	0.076 ^{ns}	0.056 ^{ns}	0.106*	-0.043 ^{ns}	0.007 ^{ns}	-0.089 ^{ns}	0.12*	0.118*	0.118*	0.122*	0.078 ^{ns}	-0.156*	1	0.073 ^{ns}	0.523**	0.468**
KWS	-0.013 ^{ns}	0.193**	0.121*	0.098 ^{ns}	0.075 ^{ns}	0.115*	0.12*	0.286**	0.291**	0.231**	0.22**	0.741**	0.173**	1	0.92**	0.892**
TKW	0.002 ^{ns}	0.22**	0.15**	0.07 ^{ns}	0.072 ^{ns}	0.107*	0.123*	0.333**	0.334**	0.259**	0.236**	0.783**	0.284**	0.81**	1	0.942**
GY	0.165**	0.175**	0.142**	0.05 ^{ns}	0.088 ^{ns}	0.042 ^{ns}	0.189**	0.314**	0.323**	0.276**	0.258**	0.665**	0.62**	0.71**	0.824**	1

ns non-significant, DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMY Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹(g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

**Highly significant, *significant

Bold indicate the diagonal that separate genotypic correlation from phenotypic correlation coefficients under drought-stressed conditions

drought tolerance in the wheat crop (Aslam et al. 2015; Bapela et al. 2022; Naeem et al. 2015; Shamuyarira et al. 2019a, b). Previous studies by Bayisa et al.(2019), Bhat-tarai et al. (2017), Bilal et al. (2015), and Allahverdiyev (2015) have reported that wheat varieties that exhibited reduced number of days to heading, maturity and grain filling period under drought-stressed could escape the adverse effects of drought. On the other hand, the obser-vation that some genotypes such as ET-13A2 and ETBW 9027 did not differ markedly in the flowering traits under well-watered and drought-stressed conditions could be considered as indication of drought tolerance (Chowdhury et al. 2021). Drought-sensitive genotypes have been reported to change to heading earlier under drought stress condition, whereas drought tolerant genotypes of wheat showed non-significant variations in heading time with changes in water availability (Chowdhury et al. 2021).

Plant height, number of tillers plant⁻¹, spike length and flag leaf area

The plant height (PH), number of tillers plant⁻¹ (NTPP), spike length (SL) and flag leaf area (FLA) of the bread wheat genotypes ranged from 70.00 cm (ETBW8984) to 113.38 cm (ETBW9406), 3.50 (ETBW8882) to 11.29 (ET13A2), 7.62 cm (WANE) to 12.13 cm (Biqa) and 26.72 cm² (ETBW8751) to 50.19 cm² (ETBW9135), respectively under well-watered condition (Tables 3

and S3). Under drought-stressed condition, PH varied from 58.97 cm (ETBW9413) to 86.47 cm (ETBW8862), NTPP from 2.00 (ETBW9412) to 6.81 (ETBW9202), SL from 6.45 cm (Menze) to 9.66 cm (Biqa) and FLA from 21.78 cm² (ETBW 9091) to 40.54 cm² (ETBW172936) (Tables 4 and S4). In this study, decrease in mean PH due to drought was 21.7%. This result is in agreement with the 20.0% reduction in plant height reported by Mushtaq et al. (2011) when irrigation was skipped at the tillering stage of crop growth. A 37.0% reduction in NTPP under drought stress relative to well-watered condition was observed in this study, which resulted in a significant reduction in grain yield. This agrees with the findings of Muhammad et al. (2022) who reported that drought stress inhibited the development of tillers per plant among the wheat genotypes by 23.7%. Selecting for taller genotypes with weightier seed would possibly increase grain yield, however, taller genotypes with heavier spike are associated with lodging under specific environmental conditions (Semahegn et al. 2020; Tadesse et al. 2019). Drought stress reduced SL by 17.20%. The results of this study shows that longer spikes produced relatively higher grain yields under well-watered and drought-stressed conditions. The mean FLA in this study was decreased by 18.8% due to drought stress.

Table 9 Genotypic correlation-based direct (on the diagonal) and indirect effects of 15 agronomic traits on grain yield of 196 bread wheat genotypes evaluated under well-watered conditions in field and greenhouse environments for two years

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
DH	-0.19	0.21	0.65	0.03	-0.05	0.22	0.16	-0.63	-0.58	0.26	-0.40	-0.17	-0.30	0.14	-0.07	0.325**
GFP	0.79	0.16	-0.79	0.07	-0.26	0.37	-0.69	0.59	0.80	-0.68	-0.12	-0.82	0.38	0.54	0.24	0.523**
DM	-0.91	0.50	0.39	0.06	-0.10	0.30	0.02	-0.29	-0.60	0.19	-0.48	-0.54	-0.27	0.68	-0.13	0.168**
PH	-0.17	-0.03	0.41	-0.33	-0.03	0.22	-0.28	0.29	0.47	0.47	0.47	-0.60	0.13	-0.09	0.10	0.16*
NTPP	-0.86	-0.92	0.23	0.07	0.15	-0.26	-0.52	0.15	0.11	0.39	0.08	-0.11	0.21	-0.21	-0.77	0.28**
SL	0.90	0.47	-0.60	-0.06	-0.16	0.37	-0.44	0.70	0.82	-0.27	0.91	0.18	0.24	-0.09	0.25	0.23**
FLA	-0.75	0.67	0.67	-0.10	0.09	0.59	0.28	0.38	0.05	0.59	0.66	0.39	0.34	-0.56	0.04	1.99**
SPS	0.47	-0.57	-0.93	0.19	-0.19	-0.79	0.05	0.39	0.74	1.00	0.41	-0.88	0.22	0.36	-0.45	0.79**
FSPS	0.58	-0.12	-0.37	0.19	-0.21	-0.80	0.08	0.34	0.46	-0.01	0.51	-0.95	0.21	0.38	0.46	0.87**
NKPS	0.58	-0.12	-0.37	0.19	-0.21	-0.80	0.08	0.34	0.68	0.12	0.58	-0.94	0.27	0.33	-0.42	0.76**
SF	0.40	0.71	-0.41	0.08	-0.32	-0.55	0.30	0.77	0.92	-0.50	0.52	-0.45	0.05	0.30	-0.19	0.72**
BMY	-0.33	-0.58	0.25	0.06	-0.10	0.06	-0.10	0.52	0.23	0.02	0.02	0.69	0.26	0.89	0.63	0.92**
HI	-0.55	0.37	0.11	-0.06	0.04	0.36	-0.40	-0.06	-0.10	0.86	-0.11	0.14	0.56	-0.36	0.28	0.75**
KWS	-0.36	-0.56	0.78	-0.14	-0.19	0.04	-0.19	0.19	0.21	-0.97	0.44	0.66	0.11	0.60	0.27	0.93**
TKW	-0.50	-0.65	0.49	-0.03	-0.10	0.26	-0.03	0.16	0.89	-0.16	0.42	0.79	-0.19	0.91	0.64	0.96**

Residual effect = 0.0251

ns non-significant, DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMY Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹ (g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

**Highly significant, *significant

Bold diagonal numbers indicated genotypic correlation-based direct effects of agronomic traits on yield under well-watered condition

Table 10 Phenotypic correlation-based direct (on the diagonal) and indirect effects of 15 agronomic traits on grain yield of 196 bread wheat genotypes evaluated under well-watered conditions in field and greenhouse environments for two years

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
DH	-0.32	0.721	0.212	0.832	0.046	0.055	-0.122	0.424	0.549	0.207	0.065	0.096	0.399	0.508	0.505	0.23**
GFP	0.054	0.21	-0.701	0.476	0.768	0.169	0.689	0.721	0.083	0.240	0.503	0.843	0.575	0.902	0.032	0.35**
DM	0.029	0.760	0.28	0.568	0.465	0.194	0.628	0.378	0.684	0.514	0.819	0.733	0.034	0.376	0.279	0.24**
PH	0.599	0.544	0.303	-0.36	0.243	0.645	-0.332	0.564	0.391	0.886	0.145	0.795	0.495	0.242	0.650	0.22**
NTPP	0.596	0.036	-0.104	0.492	0.24	0.627	0.573	-0.282	0.796	-0.622	0.816	0.145	0.479	0.772	0.401	0.08 ^{ns}
SL	0.862	0.213	0.577	0.491	0.665	0.45	-0.727	0.628	0.552	0.009	0.892	0.178	0.673	0.367	0.225	0.13 ^{ns}
FLA	0.627	0.910	0.053	0.069	-0.197	0.526	0.27	0.563	0.519	0.024	0.839	0.414	0.358	0.845	0.877	0.13 ^{ns}
SPS	0.252	0.743	0.360	0.325	0.597	0.682	0.692	0.41	0.854	0.742	0.996	0.495	0.592	0.341	0.908	0.61**
FSPS	0.036	0.446	0.887	0.905	-0.130	0.292	-0.205	0.937	0.37	0.793	0.264	0.952	0.327	0.825	0.562	0.68**
NKPS	0.539	0.413	0.028	0.594	0.231	0.608	0.315	0.839	0.190	0.48	0.086	0.196	0.829	0.167	0.639	0.57**
SF	0.943	0.008	0.319	0.720	0.722	0.800	0.103	0.424	0.565	0.824	0.16	0.552	0.089	0.364	0.154	0.69**
BMY	0.857	0.148	0.835	0.681	0.879	0.550	0.947	0.745	0.296	0.752	0.417	0.72	0.486	0.013	0.375	0.89**
HI	0.504	0.342	0.875	0.732	0.208	0.584	-0.312	0.711	0.400	0.738	0.108	0.042	0.34	0.170	0.631	0.63**
KWS	0.793	0.276	0.471	0.910	0.015	0.003	0.054	0.910	0.228	0.502	0.921	0.642	0.544	0.36	0.740	0.84**
TKW	0.293	0.105	0.139	0.382	0.533	0.571	0.603	0.916	0.784	0.971	0.869	0.079	0.927	0.942	0.52	0.88**

Residual effect = 0.0476

ns non-significant, DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMY Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹ (g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

**Highly significant, * indicates the significant correlation of agronomic traits with grain yield

Bold diagonal numbers indicated phenotypic correlation-based direct effects of agronomic traits on yield under well-watered condition

Table 11 The genotypic correlation-based direct (on the diagonal) and indirect effects of 15 agronomic traits on grain yield of 196 bread wheat genotypes evaluated under drought-stressed conditions at field and greenhouse environments for two seasons

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
DH	-0.46	-0.79	0.12	0.49	0.98	0.95	0.12	-0.90	0.90	-0.62	-0.48	0.50	0.12	-0.87	0.69	0.248**
GFP	-0.70	-0.33	0.48	-0.31	0.15	0.63	0.52	-0.14	0.75	-0.65	-0.60	0.31	0.66	-0.93	0.92	0.853**
DM	-0.66	-0.34	-0.52	0.76	0.48	0.90	0.82	-0.14	0.93	0.00	-0.86	0.29	0.80	-0.79	0.81	0.375**
PH	0.08	-0.34	0.80	-0.35	0.83	0.21	0.42	-0.93	0.96	0.34	-0.47	0.03	0.05	-0.95	0.53	0.034 ^{ns}
NTPP	-0.39	-0.25	0.65	0.35	-0.29	0.32	0.92	-0.52	0.57	-0.47	-0.38	0.74	0.47	-0.61	0.75	0.097 ^{ns}
SL	-0.80	-0.57	0.23	0.20	0.46	0.18	0.73	-0.18	0.07	-0.52	0.54	0.33	0.67	-0.78	0.97	0.09 ^{ns}
FLA	-0.82	-0.24	0.37	0.54	0.35	0.22	0.26	0.56	0.52	0.00	-0.38	0.45	0.38	-0.94	0.43	0.192**
SPS	-0.35	-0.14	0.53	0.97	0.75	0.23	0.47	0.23	0.02	-0.99	-0.57	0.60	0.90	0.34	0.67	0.715**
FSPS	-1.00	-0.86	0.28	0.66	0.62	0.40	0.22	-0.59	0.43	-0.13	-0.74	0.50	0.05	0.75	0.83	0.769**
NKPS	-0.87	-0.06	0.46	0.08	0.93	0.14	0.87	0.94	0.51	0.16	0.00	0.92	0.03	0.93	0.90	0.874**
SF	-0.53	-0.76	0.15	0.88	0.20	0.81	0.18	-0.68	0.43	-0.19	0.19	0.27	0.70	0.07	0.22	0.401**
BMY	-0.80	-0.73	0.73	0.79	0.30	0.54	0.89	-0.78	0.69	-0.09	-0.85	0.35	0.88	-0.34	0.28	0.842**
HI	-0.29	-0.88	0.78	0.83	0.27	0.18	0.63	-0.04	0.32	-0.24	-0.24	0.79	0.32	-0.38	0.68	0.468**
KWS	-0.67	-0.67	0.04	0.11	0.76	0.49	0.19	-0.90	0.32	-0.41	-0.24	0.23	0.54	0.58	0.91	0.892**
TKW	-0.42	-0.61	0.31	0.08	0.01	0.66	0.45	-0.79	0.85	-0.69	0.66	0.18	0.23	0.94	0.61	0.942**

Residual effect = 0.0323

ns non-significant, DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMY Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹ (g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

**Highly significant, * indicates the significant correlation of agronomic traits with grain yield

Bold diagonal numbers indicated genotypic correlation-based direct effects of agronomic traits on yield under drought-stressed condition

Table 12 The phenotypic correlation-based direct (on the diagonal) and indirect effects of 15 agronomic traits on grain yield of 196 bread wheat genotypes evaluated under drought-stressed conditions at field and greenhouse environments for two seasons

Traits	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMY	HI	KWS	TKW	GY
DH	-0.26	-0.21	-0.25	-0.38	-0.05	0.06	-0.12	0.24	0.25	0.21	0.10	0.55	0.51	0.60	0.51	0.45**
GFP	0.11	-0.31	0.14	0.28	0.37	-0.37	0.47	0.59	0.08	0.24	0.50	0.84	0.58	0.41	0.53	0.18*
DM	-0.40	-0.28	0.37	0.40	0.16	0.33	0.32	0.18	0.30	0.51	0.82	0.73	0.03	0.38	0.28	0.63**
PH	0.15	-0.11	0.31	-0.32	0.14	-0.13	0.13	0.26	0.17	0.89	0.15	0.80	0.50	0.24	0.65	0.42**
NTPP	0.21	-0.02	0.04	0.19	0.20	-0.27	-0.28	0.13	0.59	0.62	0.82	0.14	0.48	0.77	0.40	0.72**
SL	0.27	-0.07	-0.21	0.21	0.27	0.33	0.33	0.32	0.25	0.04	0.89	0.18	0.67	0.37	0.23	0.49**
FLA	-0.27	-0.05	0.33	0.07	-0.12	0.11	0.29	0.27	0.22	0.03	0.84	0.41	0.36	0.85	0.88	0.27**
SPS	-0.22	0.04	0.26	0.13	0.30	0.30	0.40	0.76	0.96	0.74	1.00	0.50	0.59	0.34	0.91	0.78**
FSPS	-0.16	0.09	0.20	0.41	-0.05	0.11	0.21	0.74	1.09	0.79	0.66	0.95	0.33	0.25	0.56	0.46**
NKPS	-0.20	0.02	0.09	0.44	-0.13	0.12	0.14	0.38	1.65	0.36	0.89	0.20	0.83	0.17	0.64	0.98**
SF	0.34	0.04	0.15	0.32	0.13	0.10	0.10	0.16	1.60	0.83	0.92	0.55	0.19	0.37	0.50	0.38**
BMY	0.26	-0.09	0.16	0.42	0.48	0.50	0.45	0.51	0.63	0.35	0.42	0.65	0.49	0.01	0.38	0.93**
HI	0.21	0.08	0.09	0.49	0.08	0.31	0.31	0.21	0.25	0.34	0.56	0.04	0.43	0.17	0.63	0.88**
KWS	0.33	0.05	0.07	0.41	0.17	0.25	0.31	0.51	0.61	0.18	0.92	0.96	0.54	0.46	0.74	0.49**
TKW	0.29	0.14	0.11	0.38	0.24	0.30	0.37	0.59	0.70	0.21	0.87	0.88	0.93	0.94	0.55	0.89**

Residual effect = 0.069

ns non-significant, DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMY Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹ (g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

**Highly significant, *significant

Bold diagonal numbers indicated phenotypic correlation-based direct effects of agronomic traits on yield under drought-stressed condition

Number of spikelets spike⁻¹, fertile spikelets spike⁻¹, number of kernels spike⁻¹ and spike fertility

Under well-watered condition, genotype ETBW172938 had the highest number of spikelets spike⁻¹ (SPS, 30.60), fertile spikelets spike⁻¹ (FSPS, 28.60), number of kernels spike⁻¹ (NKPS, 85.80) and spike fertility (SF, 93.5%), whereas genotype ETBW9441 had the lowest values of 21.66, 18.65, 57.00 and 86.1%, for the same traits, respectively (Tables 3 and S3). Under drought-stressed condition, genotype ETBW172938 recorded the highest SPS (25.17), FSPS (22.98) and NKPS (70.75), whereas genotype ETBW9441 had the lowest SPS (19.84), FSPS (17.44) and NKPS (53.77) and. Genotype ETBW9202 had the highest SF (83.92%), while the lowest (72.61%) was recorded by genotype ETBW9441 (Tables 4 and S4). On the average, drought stress reduced SPS by 11.4%, while FSPS, NKPS and SF were reduced by 12.2%, 11.5%, and 10.4%, respectively. Muhammad et al. (2022) had earlier reported 32.1% reduction in number of fertile spikes for some wheat genotypes due to moisture stress. Similarly, Tefera et al. (2021) reported that drought stress reduced number of spikelets spike⁻¹ by 23.0%. A 48.0% and 29.0% of reduction in number of kernels spike⁻¹ and spikelet fertility, respectively was reported in some wheat genotypes (Prasad et al. 2011) under drought-stress, whereas Afzal et al. (2017) reported 38.1% reduction in number of grains spike⁻¹.

Kernel weight spikes⁻¹ (g) and one thousand kernel weight (g)

Under well-watered condition, kernel weight spike⁻¹ (KWS) ranged from 1.75 g for genotype ETBW9435 to 4.40 g for genotype ETBW172938. One thousand kernel weight (TKW) varied from 30.32 g for ETBW9441 to 58.62 g for genotype Alidoro with a mean of 43.03 g. Under drought-stressed condition, KWS was highest for genotype Dinknesh (3.43 g) and lowest for genotypes ETBW8944 and ETBW 9435 (1.55 g). The range in TKW under drought-stressed condition was 23.11 g for genotype ETBW 9441 to 40.85 g for genotype Dinknesh with a mean of 32.59 g. Drought stress reduced TKW by 23.9%. Our findings is consistent with results of Sher et al. (2017) and Thungo et al. (2020) on the reduction of one thousand kernel weight by drought stress.

Biomass yield (t ha⁻¹), harvest index and grain yield (t ha⁻¹)

The bread wheat genotypes differed significantly for biomass yield (BMY), harvest index (HI) and grain yield (GY). Averaged across genotypes, BMY and HI were 10.01 t ha⁻¹ and 37.4%, under well-watered condition, and 7.95 t ha⁻¹ and 30.9% under drought-stressed condition, respectively. The GY of the genotypes under well-watered condition ranged from 2.52 t ha⁻¹ for genotype Menze to 5.06 t ha⁻¹ for genotype Alidoro with a mean of 3.76 t ha⁻¹. Under drought-stressed condition, the range

Table 13 Clustering of the 196 bread wheat genotypes using agronomic traits under well-watered conditions

Cluster	Number of Genotypes	Name of Genotypes in each cluster									
1	24	Abola	Dinknesh	ETBW172864	ETBW172872	ETBW172955	ETBW8303	ETBW8311	ETBW8394	ETBW8659	
		ETBW8725	ETBW8735	ETBW8772	ETBW8816	ETBW8862	ETBW8996	ETBW9083	ETBW9084	ETBW8676	
		ETBW9104	ETBW9107	ETBW9134	ETBW9140	ETBW9220	ETBW9383				
2	43	ETBW9410	ETBW9422	ETBW9087	ETBW9091	ETBW9436	ETBW9470	Dandaa	Dure	Enkoy	
		ETBW172082	ETBW172996	ETBW8260	ETBW8261	ETBW8484	ETBW8486	ETBW8492	ETBW8577	ETBW8584	
		ETBW8640	ETBW8654	ETBW8661	ETBW8668	ETBW8684	ETBW8777	ETBW8817	ETBW8823	ETBW8826	
		ETBW8827	ETBW8831	ETBW8840	ETBW8882	ETBW8901	ETBW8905	ETBW8987	ETBW9001	ETBW9019	
		ETBW9066	ETBW9068	ETBW9089	ETBW9092	ETBW9093	ETBW9095	ETBW9108			
3	44	ETBW9109	ETBW9110	ETBW9112	ETBW9135	ETBW9138	ETBW9139	ETBW9169	ETBW8489	ETBW9177	
		ETBW9183	ETBW9200	ETBW9221	ETBW9233	ETBW9294	ETBW9295	ETBW9305	ETBW8800	ETBW9404	
		ETBW9407	ETBW9411	ETBW9412	ETBW9416	ETBW9424	ETBW9438	ETBW9445	ETBW8923	ETBW9102	
		ETBW9175	ETBW9396	ETBW9402	ETBW9473	ETBW9484	Gasay	Hidasie	Millennium	Mitike	
		K62954A	Kakaba	Kingbird	Kubsa	MadaWelabu	LEMU	Manduyo	Pavon76		
4	23	Sirbo	Sulla	Tossa	Tsehay	Tusie	Alidoro	Bolo	Dashen	ET13A2	
		ETBW172936	ETBW172938	ETBW8491	ETBW8583	ETBW8870	ETBW9027	ETBW9029	ETBW9088	ETBW9137	
		ETBW9202	ETBW9406	Digelu	ETBW8597	ETBW8820					
5	28	ETBW8903	ETBW8907	ETBW8908	ETBW9176	ETBW9185	ETBW9378	ETBW9413	ETBW9444	ETBW9449	
		ETBW9450	Galema	Gambo	Hoggana	Honqolo	Huluka	Menze	Meraro	Ogolcho	
		Shorima	Tay	Laketch	Kulkulu	Biqa	Bobicho	Dereselign	Doddota	ETBW172862	
		ETBW8070									
6	34	ETBW8289	ETBW8585	ETBW8675	ETBW8797	ETBW8818	ETBW8881	ETBW8944	ETBW8945	ETBW8974	
		ETBW8981	ETBW8983	ETBW8984	ETBW9091	ETBW9179	ETBW9180	ETBW9184	ETBW9279	ETBW9384	
		ETBW9409	ETBW9414	ETBW9433	ETBW9440	ETBW9441	ETBW8751	ETBW9026	ETBW9435	Galil	
		Hawii	K6290Bulk	Katar	KBG01	Simba	Sofumar	WANE			

Table 14 Cluster means of agronomic traits for 196 bread wheat genotypes under well-watered conditions

Cluster	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMV	HI	KWS	TKW	GY
1	63.23	55.71	118.95	108.19	6.49	9.61	36.64	26.07	23.87	73.00	91.37	10.81	37.85	3.20	46.32	4.07
2	62.95	55.44	118.38	94.94	6.15	9.22	41.30	24.56	22.11	67.97	89.83	9.89	36.78	2.70	42.26	3.64
3	59.73	56.38	116.11	90.21	6.15	9.40	36.52	25.84	23.64	72.46	91.31	10.70	38.32	3.20	46.59	4.11
4	72.24	52.83	124.98	87.97	6.02	8.82	36.04	24.43	22.03	67.82	90.01	9.76	37.95	2.71	41.79	3.68
5	61.83	53.90	115.82	82.05	5.34	9.29	36.97	23.58	21.08	64.80	89.24	9.47	36.89	2.55	40.15	3.48
6	60.75	56.21	116.93	98.47	6.37	9.48	32.71	23.91	21.32	65.36	89.08	9.58	36.70	2.57	40.27	3.51

DH Days to heading, *GFP* Grain filling period (days), *DM* Days to maturity, *PH* Plant height (cm), *NTPP* Number of tillers plant⁻¹, *SL* Spike length (cm), *FLA* Flag leaf area (cm²), *SPS* Spikelets spike⁻¹, *FSPS* Fertile spikelets spike⁻¹, *NKPS* Number of kernels spike⁻¹, *SF* Spike fertility (%), *BMV* Biomass yield (t ha⁻¹), *HI* Harvest index (%), *KWS* Kernels weight spike⁻¹ (g), *TKW* Thousand kernels weight (g), and *GY* Grain yield (t ha⁻¹)

in GY was 1.96 t ha⁻¹ for genotype Galema to 3.84 t ha⁻¹ for genotype Alidoro with a mean of 2.64 t ha⁻¹. Mean GY reduction due to drought stress was 29.8%. It should be noted that under both conditions, genotype Alidoro had the highest GY and can be used in drought tolerance breeding. Low grain yields in drought stress environments are indications of drought stress susceptibility to drought. Bread wheat genotypes able to maintain high thousand-kernel weight and grain yield under moisture

limited environments could possess high level of drought stress tolerance (Bayisa et al. 2019).

Estimates of variance components, heritability and genetic advance

The estimates of genotypic (σ^2_g), phenotypic (σ^2_p), and environmental (σ^2_e) variances, genotypic coefficients of variation (GCV), phenotypic coefficients of variation (PCV), environmental coefficients of variation (ECV),

Table 15 Distribution of 196 bread wheat genotypes in five clusters using agronomic traits under drought-stressed condition

Cluster	Number of Genotypes	Name of Genotypes in each cluster
1	50	Abola Dinknesh ETBW8772 ETBW8816 ETBW9102 ETBW9104 ETBW9436 ETBW9470 ETBW8901 ETBW8901 ETBW9176 ETBW9177 ETBW9294 ETBW9221 ETBW9449 ETBW9450 K6295-4A Kulkulu ETBW8684 ETBW8881 ETBW8903 ETBW9091 ETBW9378 Menze ETBW8597 ETBW8881 ETBW8903 ETBW9091 ETBW9441 K6295-4A Menze Biq ETBW8584 ETBW8492 ETBW8800 ETBW8817 ETBW8923 ETBW9138 ETBW9110 ETBW9396 ETBW172082 Manduyo Shorima ETBW172862 ETBW9402 ETBW9404 ETBW172864 Sirbo ETBW8070 ETBW8491 ETBW8491 ETBW172936 ETBW8735 ETBW9088 ETBW9087 ETBW9410 ETBW9422 ETBW8820 ETBW9175 ETBW8725 ETBW9087 ETBW9410 ETBW9295 Digelu ETBW8261 ETBW9109 ETBW9108 ETBW9095 ETBW9424 ETBW9438 ETBW9444 Dereseign Doddota ETBW8289 ETBW8070 ETBW8945 ETBW8974 ETBW8981 ETBW9435 Huluka Honqolo ETBW8484 ETBW8486 ETBW8676 Katar ETBW8882 ETBW9093 ETBW9279 ETBW9383 ETBW9416 ETBW9484 Kingbird Kubsa Tsehay ETBW9027 ETBW8870 ETBW8583 ETBW9137
2	32	ETBW8311 ETBW9029 ETBW9135 ETBW172955 ETBW9089 ETBW9200 ETBW9413 Hoggana Meraro ETBW8818 ETBW8944 ETBW9409 Gambo Simba ET-13A2 ETBW8661 ETBW8827 ETBW9026 ETBW9169 ETBW9411 Hidasie Tay ETBW8583
3	32	ETBW8394 ETBW8996 ETBW9134 ETBW172938 ETBW9066 ETBW9185 ETBW9384 Gasay LEMU ETBW8797 ETBW8908 ETBW9184 Galli Pavon-76 Dure ETBW8653 ETBW8826 ETBW9019 ETBW9140 ETBW9407 ETBW172996 Sulla ETBW8491
4	27	ETBW8303 ETBW8862 ETBW9112 ETBW172872 ETBW8987 ETBW9180 ETBW9305 ETBW9473 Laketch ETBW8751 ETBW8907 ETBW9179 Galerma Mitikie Danda'a ETBW8640 ETBW8823 ETBW9001 ETBW9139 ETBW9404 ETBW172864 Sirbo ETBW8070 ETBW8491 ETBW8491 ETBW172936
5	26	ETBW8303 ETBW8862 ETBW9112 ETBW172872 ETBW8987 ETBW9180 ETBW9305 ETBW9473 Laketch ETBW8751 ETBW8907 ETBW9179 Galerma Mitikie Danda'a ETBW8640 ETBW8823 ETBW9001 ETBW9139 ETBW9404 ETBW172864 Sirbo ETBW8070 ETBW8491 ETBW8491 ETBW172936
6	29	ETBW8303 ETBW8862 ETBW9112 ETBW172872 ETBW8987 ETBW9180 ETBW9305 ETBW9473 Laketch ETBW8751 ETBW8907 ETBW9179 Galerma Mitikie Danda'a ETBW8640 ETBW8823 ETBW9001 ETBW9139 ETBW9404 ETBW172864 Sirbo ETBW8070 ETBW8491 ETBW8491 ETBW172936

Table 16 Cluster means of agronomic traits for 196 bread wheat genotypes under drought-stressed conditions

Cluster	DH	GFP	DM	PH	NTPP	SL	FLA	SPS	FSPS	NKPS	SF	BMV	HI	KWS	TKW	GY
1	60.57	57.47	118.04	66.13	3.45	7.64	32.21	22.40	20.07	62.30	80.87	8.58	34.51	2.75	36.81	3.48
2	62.97	54.69	117.66	65.01	3.49	7.78	29.81	21.12	18.79	58.27	80.36	7.69	32.52	2.06	29.32	2.98
3	71.20	54.10	125.29	69.47	3.41	7.69	30.52	21.98	19.77	61.13	80.88	8.08	34.11	2.37	32.92	3.27
4	61.39	57.32	118.71	77.27	3.39	8.02	26.26	21.26	18.89	58.28	80.29	7.89	32.85	2.21	31.25	3.08
5	63.96	57.05	121.00	82.48	4.02	7.58	30.66	22.67	20.36	62.96	81.09	8.70	33.98	2.71	36.32	3.47
6	61.06	57.10	118.16	73.38	3.64	7.52	30.44	22.10	19.81	61.34	80.94	8.48	33.75	2.57	35.31	3.37

DH Days to heading, GFP Grain filling period (days), DM Days to maturity, PH Plant height (cm), NTPP Number of tillers plant⁻¹, SL Spike length (cm), FLA Flag leaf area (cm²), SPS Spikelets spike⁻¹, FSPS Fertile spikelets spike⁻¹, NKPS Number of kernels spike⁻¹, SF Spike fertility (%), BMV Biomass yield (t ha⁻¹), HI Harvest index (%), KWS Kernels weight spike⁻¹ (g), TKW Thousand kernels weight (g), and GY Grain yield (t ha⁻¹)

Table 17 Eigen vectors associated with the first five principal components and the proportion and cumulative contributions for 16 agronomic and yield traits of 196 bread wheat genotypes evaluated in 2021 and 2022 under well-watered conditions

Traits	Principal components				
	PC1	PC2	PC3	PC4	PC5
Days to heading	-0.03	-0.68	-0.13	0.04	-0.05
Grain filling period	0.14	0.38	-0.19	-0.17	0.07
Days to maturity	0.07	-0.57	-0.28	-0.08	-0.01
Plant height	0.11	0.09	-0.52	0.22	-0.15
Number of tillers plant ⁻¹	0.08	-0.02	-0.33	0.53	0.18
Spike length	0.03	0.20	-0.37	0.38	0.19
Flag leaf area	0.01	-0.06	-0.11	-0.33	0.90
Number of spikelets spike ⁻¹	0.35	-0.01	-0.11	-0.13	-0.03
Fertile spikelets spike ⁻¹	0.36	-0.01	-0.09	-0.13	-0.03
Number of kernels spike ⁻¹	0.36	-0.02	-0.07	-0.12	-0.02
Spike fertility	0.34	-0.02	0.01	-0.11	-0.05
Biomass yield	0.33	0.01	0.01	-0.08	-0.11
Harvest index	0.13	-0.12	0.47	0.50	0.27
Kernels weight spike ⁻¹	0.35	-0.02	0.05	-0.03	-0.03
Thousand kernels weight	0.33	0.00	0.18	0.09	0.01
Grain yield	0.33	-0.04	0.25	0.23	0.08
Eigen values	7.00	2.03	1.29	1.25	0.98
Explained variance (%)	43.73	12.70	8.04	7.80	6.15
Cumulative variance (%)	43.73	56.43	64.48	72.28	78.42

Eigen vectors ≥ 0.20 , which mainly controlled each principal component axes are in bold

broad-sense heritability (H²_b), genetic advance (GA) and genetic advance as percent of mean (GAM) of 16 agronomic traits of 196 bread wheat genotypes under well-watered and drought-stressed conditions are presented in Tables 5 and 6, respectively.

Under well-watered conditions, genotypic variances for all the traits were higher than the variances due to environment. The estimates of PCV were higher than the respective GCVs for all the traits. The PCV and GCV

were highest for KWS and lowest for SF. The PCV for the traits were high, except for DM, NKPS and SF which had moderate values. Similarly, GCV values for the traits were high, except for DM, PH, NKPS and SF which had moderate values. Broad-sense heritability estimates for the traits ranged from moderately high to very high and were in all cases accompanied by high genetic advance as percent of mean.

Under drought-stressed conditions, genotypic variances for all the traits were similarly, higher than the variances due to environment effects. The PCV and GCV were highest for KWS and lowest for SF. Moderate PCV estimates were obtained for DM, NKPS and SF, while all the other traits exhibited high PCV values. The GCV for the traits were high, except for GFP, DM, NKPS and SF which had moderate values. Except for NTPP which had medium broad-sense heritability estimate, the estimates for the traits ranged from moderately high to very high and were also accompanied by high genetic advance as percent of mean.

In this study, the higher PCV than GCV values for all the studied traits under both water regimes, indicated a greater influence of environment on the expression of the traits. The high PCV and GCV estimates recorded for most of the traits, is in close agreement with the findings of earlier authors (Malbhage et al. 2020; Jahan et al. 2020; Singh et al. 2020) who reported high estimates of PCV and GCV for agronomic traits in wheat. The magnitude of heritability estimates under drought-stressed condition were slightly higher than under well-watered condition suggesting that selection of genotypes for their reaction to moisture could be easier under drought-stressed condition. Similar results of high heritability estimates under drought-stressed condition in wheat have been reported by Singh et al. (2020), which implies that selection of genotype under drought would be effective. High heritability estimates alone may not be adequate in predicting the breeding value of a genotype, but denotes the amount of genetic variation that is expressed in the phenotype. Genetic advance as percent of mean helps to

Table 18 Eigen vectors associated with the first five principal components and the proportion and cumulative contributions for 16 agronomic and yield traits of 196 bread wheat genotypes evaluated in 2021 and 2022 under drought-stressed condition

Traits	Principal components				
	PC1	PC2	PC3	PC4	PC5
Days to heading	-0.00	0.67	-0.01	-0.14	0.08
Grain filling period	0.11	-0.42	-0.15	-0.06	0.05
Days to maturity	0.08	0.54	-0.12	-0.22	0.14
Plant height (cm)	0.09	-0.12	-0.29	-0.49	0.35
Number of tillers plant ⁻¹	0.09	-0.02	-0.29	-0.23	-0.06
Spike length	0.07	-0.14	-0.10	-0.01	0.79
Flag leaf area (cm ²)	0.06	0.07	0.28	0.55	0.39
Number of spikelets spike ⁻¹	0.35	0.07	-0.16	0.27	0.02
Fertile spikelets spike ⁻¹ (%)	0.36	0.07	-0.20	0.25	-0.01
Number of kernels spike ⁻¹	0.36	0.09	-0.20	0.25	-0.03
Spike fertility (%)	0.28	0.08	-0.32	0.04	-0.13
Biomass yield (t ha ⁻¹)	0.34	-0.09	0.02	-0.13	-0.13
Harvest index (%)	0.16	0.08	0.53	-0.22	0.13
Kernels weight spike ⁻¹ (g)	0.36	-0.06	0.19	-0.06	-0.06
Thousand kernels weight (g)	0.34	-0.11	0.24	-0.20	-0.10
Grain yield (t ha ⁻¹)	0.33	-0.02	0.36	-0.17	0.01
Eigen values	6.28	2.15	1.42	1.27	1.04
Explained variance (%)	39.25	13.42	8.86	7.94	6.53
Cumulative variance (%)	39.25	52.67	61.53	69.47	76.00

Eigen vectors ≥ 0.20 , which mainly controlled each principal component axes are in bold

estimate the expected response to selection for a certain trait. Since high heritability values may not always be associated with high genetic advance (Amin et al. 1992), better genetic gain through selection would be achieved when traits exhibit high heritability accompanied with high genetic advance (Johnson et al. 1955). Therefore, occurrence of moderate to high heritability values and high genetic advance for most of the agronomic and yield traits under both water regimes suggest the presence of additive gene action for the traits, indicating that selection for the traits will lead to genetic gain (Jatoi et al. 2012; Rani et al. 2018). Moderate to high heritability estimates coupled with high genetic advance as percent of mean had been reported by other authors (Pradhan et al. 2019; Hossain et al. 2021; Lamara et al. 2022) for most agronomic and yield traits in bread wheat.

Genotypic and phenotypic correlations and path coefficients

Genotypic and phenotypic correlations

Genotypic and phenotypic correlation coefficients explaining the degree of relationships among grain yield and agronomic traits of bread wheat genotypes under well-watered and drought-stressed conditions are

presented in Tables 7 and 8. Agronomic traits like early heading, anthesis and maturity, and root system are key traits for cultivar development to improve drought tolerance and increase yield gains under drought-stressed conditions (Bhattarai et al. 2017; Sher et al. 2017; Thungo et al. 2020). In the present study, values for genotypic correlation coefficients were higher than their corresponding phenotypic correlation coefficients for most of the studied traits, indicating that the associations were largely due to genetic causes. The results of this study are similar to the earlier findings of (Bayisa and Amanuel 2021).

Under well-watered conditions, highly significant and positive genotypic and phenotypic correlations were observed between GY on the one hand, and DH, GFP, SPS, FSPS, NKPS, SF, BMY, HI, KWS and TKW. Whereas the genotypic correlations between GY on the one hand and DM, PH, NTPP, FLA and SL were positive and significant, the phenotypic correlations between GY and the same traits were not significant. Under drought-stressed conditions, the genotypic and phenotypic the associations between GY and DH, GFP, DM, FLA, SPS, FSPS, NKPS, SF, BMY, HI, KWS and TKW were positive and highly significant. However, PH, NTPP and SL were not significantly correlated with GY. In this study, the strongest and highest values for genotypic and phenotypic correlation were between GY on the one hand and TKW, KWS and BMY under both well-watered and drought-stressed conditions. These suggested that the traits could be helpful in selecting drought-tolerant genotypes with increased GY. Mahpara et al. (2022) reported that GY was positively correlated with PH, SL, SPS, FLA, NKPS, and TKW which supports the findings in this study. Semahegn et al. (2021) reported that GY exhibited the strongest association with TKW under both drought-stressed and non-stressed conditions, consistent with our findings. The DH and DM exhibited strong positive genotypic and phenotypic correlations with each other under well-watered and drought-stressed conditions.

Genotypic and phenotypic correlation-based path coefficients

Genotypic and phenotypic correlation-based direct and indirect effects of agronomic traits on grain yield under well-watered and drought-stressed conditions are presented in Tables 9, 10, 11 and 12, respectively. Path coefficient analysis partitions the total correlation between independent variables and a dependent variable into components of direct and indirect effects (Khan 2012). Under well-watered conditions, based on genotypic and phenotypic correlations all the traits, except DH and PH, exhibited positive direct effects on GY. Genotypically,

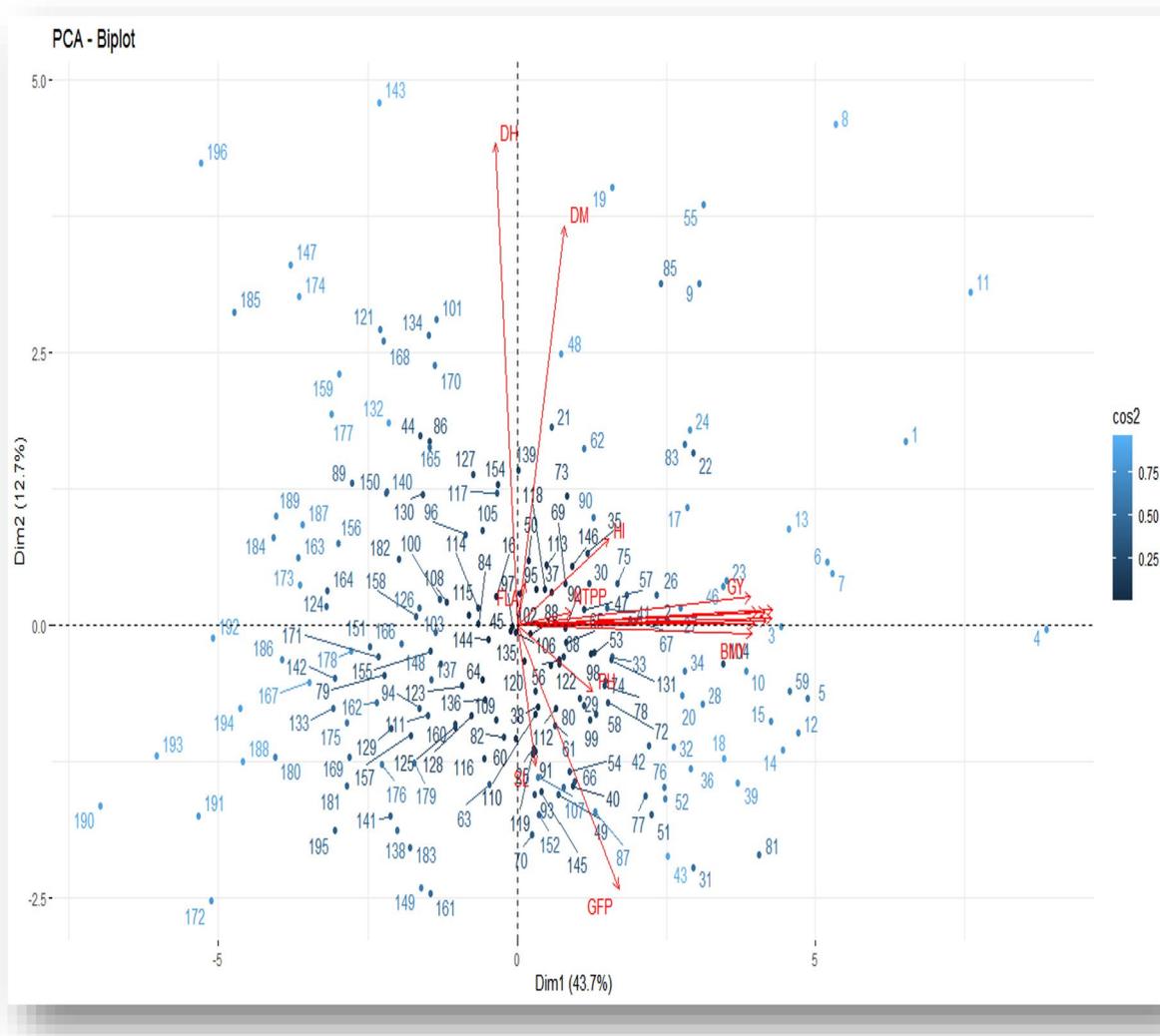


Fig. 1 PCA-biplot grouping of 196 bread wheat genotypes evaluated in 2021 and 2022 in terms of genotype × traits under well-watered conditions. *DH* Days to heading, *GFP* Grain filling period (days), *DM* Days to maturity, *PH* Plant height (cm), *NTPP* Number of tillers plant⁻¹, *SL* Spike length (cm), *FLA* Flag leaf area (cm²), *SPS* Spikelets spike⁻¹, *FSPS* Fertile spikelets spike⁻¹, *NKPS* Number of kernels spike⁻¹, *SF* Spike fertility (%), *BMY* Biomass yield (t ha⁻¹), *HI* Harvest index (%), *KWS* Kernels weight spike⁻¹ (g), *TKW* Thousand kernels weight (g), and *GY* Grain yield (t ha⁻¹). Colored dots (.) with corresponding numbers represent genotypes

BMY had the highest positive and direct effect on GY, followed by TKW, KWS, HI, SF, FSPS, SPS, DM and SL. These traits had highly significant positive genotypic correlations with GY and can be used to advance an effective selection for improving the GY of bread wheat genotypes. The previous findings of Gashaw et al. (2010) revealed that BMY (1.08) and HI (0.69) exerted high positive genotypic direct effect on GY, which supports the results of this study. Based on phenotypic correlations, BMY, TKW, NKPS, SL, SPS, FSPS, KWS and HI had high positive direct effects on GY. Baye et al. (2020) had

earlier reported that GFP, NKPS, BMY and HI showed positive direct effect on GY at phenotypic levels. Furthermore, the findings of this study are in agreement with the works of Dukamo et al. (2023) and Iftikhar et al. (2012) who reported that the SPS and NKPS showed direct positive phenotypic effects on GY under irrigated condition. Based on the residuals the agronomic traits included in path coefficient analysis explained 97.5% and 95.2% of the variability in GY at genotypic and phenotypic levels, respectively under well-watered conditions.

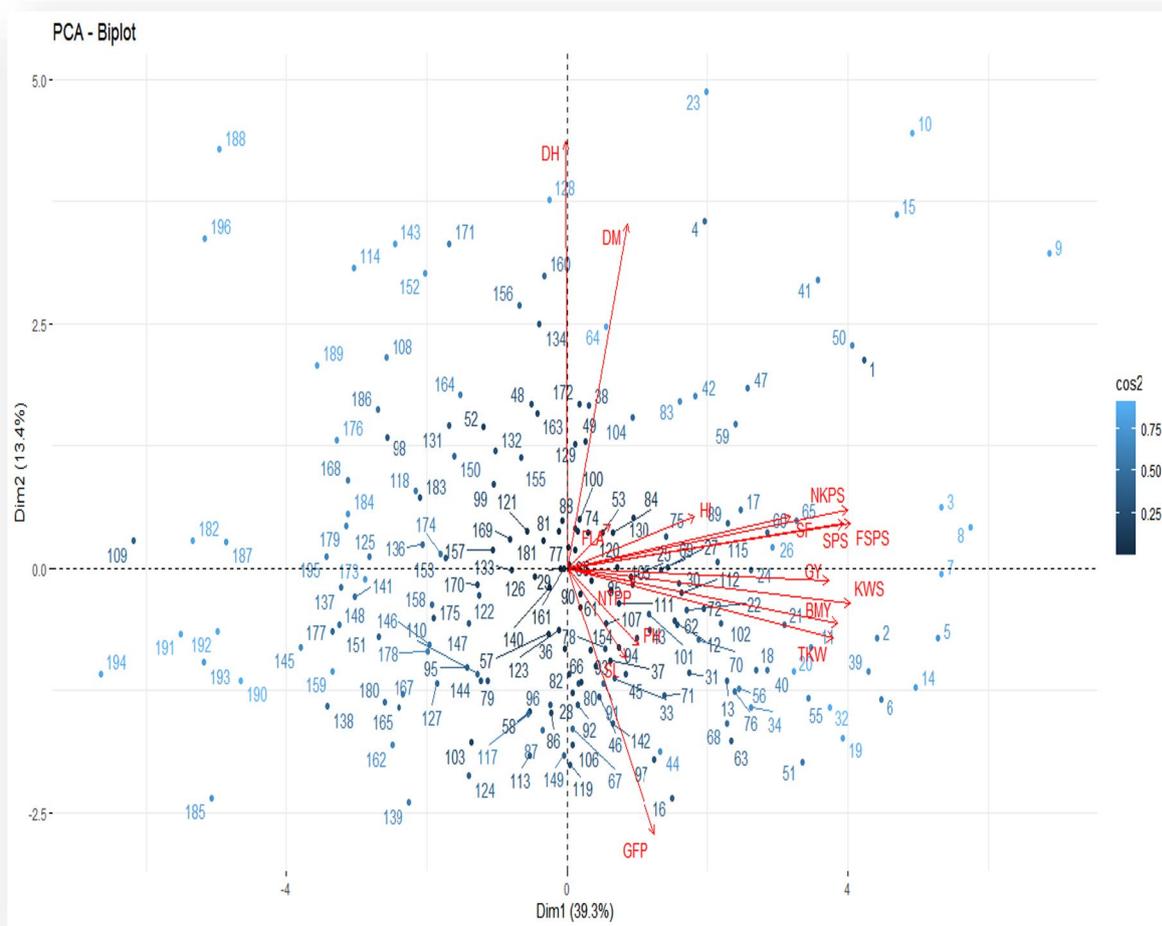


Fig. 2 PCA-biplot grouping of 196 bread wheat genotypes evaluated in 2021 and 2022 in terms of genotype × traits under drought-stressed conditions. *DH* Days to heading, *GFP* Grain filling period (days), *DM* Days to maturity, *PH* Plant height (cm), *NTPP* Number of tillers plant⁻¹, *SL* Spike length (cm), *FLA* Flag leaf area (cm²), *SPS* Spikelets spike⁻¹, *FSPS* Fertile spikelets spike⁻¹, *NKPS* Number of kernels spike⁻¹, *SF* Spike fertility (%), *BMY* Biomass yield (t ha⁻¹), *HI* Harvest index (%), *KWS* Kernels weight spike⁻¹ (g), *TKW* Thousand kernels weight (g), and *GY* Grain yield (t ha⁻¹). Colored dots (.) with corresponding numbers represent genotypes

Under drought-stressed condition, TKW manifested the highest positive genotypic direct effect on GY, followed by KWS and FSPS. The TKW also exhibited positive indirect effects on GY through KWS, FSPS, SL, SE, FLA, DM, HI, and BMY. On the other hand, FSPS recorded the highest positive phenotypic direct effect on GY followed by SF and SPS. The FSPS also showed high positive indirect effects on GY through BMY, NKPS, SPS, SE, TKW, PH and HI. The SF exerted positive and high phenotypic indirect effects on GY through FSPS, NKPS, BMY, TKW, KWS, DH and PH. The SPS showed high positive phenotypic indirect effects on GY through SE, FSPS, TKW, NKPS, HI, BMY, FLA, KWS, SL and NTPP. In contrast, DH, GFP and PH exhibited moderate to high negative direct effect on GY.

The high positive genotypic and phenotypic direct effects of FSPS, TKW, KWS, BMY and HI coupled with high genotypic and phenotypic correlations on GY, indicated selection based on this trait would be effective to obtain drought tolerant bread wheat genotypes under drought-stressed condition. Baye et al. (2020) reported that HI exerted the highest positive direct effect on GY, followed by BMY, which agreed with the findings of this study. Hence, selection based on this trait would be effective to improve grain yield. From the residuals, under drought-stressed condition the traits explained 96.8% (genotypic) 93.1% (phenotypic) of the variation in bread wheat GY.

Cluster analysis

Under both well-watered and drought-stressed conditions, the 196 bread wheat genotypes were grouped into six clusters. Under well-watered condition (Tables 13 and 14), cluster 3 was the largest with 44 genotypes, representing 22.5% of genotypes, followed by cluster 2 with 43, cluster 6 with 34, cluster 5 with 28, cluster 1 with 24 and cluster 4 with 23 genotypes (Table 13). Cluster 1 comprised of genotypes that exhibited long PH and SL, and high NTPP, SPS, NKPS, SF, BMY and KWS. The genotypes in cluster 2 were characterised by large FLA. Cluster 3 consisted of genotypes with long GFP, high KWS, TKW and GY with early DH. The genotypes in cluster 4 were characterised by long DH and DM, short GFP and SL. The genotypes in cluster 5 had short DM and PH, and were low in NTPP, FSPS, BMY, KWS, TKW and GY. Cluster 6 comprised of genotypes that had small FLA, and were low in SF and HI.

Under drought-stressed conditions (Tables 15 and 16), cluster 1 comprised of 50 genotypes, while clusters 2, 3, 4, 5 and 6 had 32, 32, 27, 26 and 29 genotypes, respectively. The genotypes in cluster 1 were characterised by short DH, long GFP, large FLA and high HI, KWS, TKW and GY. Cluster 2 comprised of genotypes that had short DM and PH with low SPS, FSPS, NKPS, BMY, HI, KWS, TKW and GY. The genotypes in cluster 3 were characterised by long DH and DM with short GFP. Cluster 4 consisted of genotypes that had small NTPP, FLA and SF, whereas genotypes in cluster 5 had long PH, high NTPP, SF and BMY, and intermediate in other traits. The genotypes in cluster 6 were short in SL and intermediate in other traits.

Genotypes that had the highest grain yields under the two water regimes such as Alidoro, Bolo, Dashen, ETBW8491, ETBW8583, ETBW8870, ETBW9027, ETBW9137, ETBW9202, ETBW9406 and ETBW172936 would be valuable in breeding efforts aimed at the development of genotypes with novel drought stress tolerance related traits. The studies of Grzesiak et al. (2019) and Mohi-ud-din et al. (2021) had also reported the utility of cluster analysis in discriminating among bread wheat genotypes based on drought tolerance indices.

Principal component analysis and genotype by trait biplot analysis

Under well-watered condition, the first five principal components (PCs) accounted for 78.4% of the total variation among the genotypes, with PC1 accounting for more than half (43.7%) of the variation (Table 17). The first PC was positively discriminated by number of SPS, FSPS, NKPS, SF, BMY, KWS, TKW and GY. The second PC which accounted for 12.7% of the total variation was positively associated with GFP and SL, however, DH and DM contributed negatively. The major

positive contributors to the third PC which accounted for 8.0% of the variation, were HI and GY, whereas DM, PH, NTPP and SL contributed negatively. The fourth PC which accounted for 7.8% of the variation, was positively related with PH, NTPP, SL, HI and GY, while the major negative contributor was FLA. The proportion of variation accounted for by the fifth PC was 6.2%, and was positively discriminated by FLA and HI.

Under drought-stressed condition, the first five PCs accounted for 76.0% of the total variation among the genotypes, with the first and second PCs cumulatively explaining 52.7% of the total variance (Table 18). The first PC explained 39.3% of the total variance, and similar to the well-watered condition, the major positive contributors were number of SPS, FSPS, NKPS, SF, BMY, KWS, TKW and GY. The second PC which accounted for 13.4%, was positively associated with DH and DM, whereas GFP was negatively associated. The third, fourth and fifth PCs accounted for 8.9%, 7.9%, and 6.5%, respectively of the total variability.

The associations among the different traits and bread wheat genotypes with principal components were further represented using a biplot of the first and second PCs. Under well-watered condition, the PCA biplot (Fig. 1) revealed that with the exception of DH, all other traits contributed positively to the first PC. On the second PC, the contributions of other traits were positive, except GFP, PH, SL and BMY which contributed negatively. Based on vector lengths, the contributions of FLA and NTPP were very low to the first and second PCs (Fig. 1). Under drought-stressed condition, the PCA biplot revealed that all the traits contributed positively to the first PC, with the exception of DH (Fig. 2). On the other hand, GFP, PH, SL, NTPP, KWS, TKW, BMY and GY made negative contributions to the second PC, whereas the contributions of other traits were positive. Also, based on vector lengths, FLA made the least contribution to the two PCs. A PCA-biplot analysis can be exploited to select traits that can be classified into main clusters and sub clusters based on homogeneity and dissimilarity (Mohi-ud-din et al. 2021).

Conclusions

Drought stress is a complex trait, which is controlled by several major and minor genes that influence the crop's adaptability. In the present study, 196 genetically diverse genotypes of bread wheat were evaluated under drought-stressed and well-watered conditions. The bread wheat genotypes exhibited a wide range of noticeable genetic variation for all the traits studied under both water regimes, an indication that the tested genotypes comprised of adequate genetic resources for the development of drought tolerant genotypes. Relative to well-watered

condition, drought stress significantly reduced all the traits, except days to heading, which was delayed. Fertile spikelets spike⁻¹, one thousand kernel weight, number of kernels spike⁻¹, biomass yield and harvest index had high positive genotypic and phenotypic correlations and direct effects on grain yield, indicating selection based on these traits would be effective for the improvement of grain yield in bread wheat. Eight genotypes namely Alidoro, Dinknesh, Bolo, ET13A2, ETBW8996, ETBW172938, ETBW9088 and ETBW8870 were found to produce high stable yields under both well-watered and drought-stressed conditions. High broad-sense heritability estimates and genetic advance was exhibited for GY under both water regimes, which indicated the predominance of additive gene effects in its regulation and create opportunity to conduct effective selection. The identified genotypes could serve as a rich genetic resource for sustainable bread wheat production and effective breeding under adequate and marginal growing conditions in Ethiopia.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43170-024-00259-6>.

Supplementary Material 1: Table S1. Monthly weather data during crop season (2020/2021 and 2021/2022) at Wachemo University, Hosanna.

Supplementary Material 2: Table S2. List of genotypes used in the study.

Supplementary Material 3.

Supplementary Material 4.

Author contributions

BMS: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software validation, visualization, writing original draft preparation; AA: Conceptualization, project administration, supervision, review & editing.

Availability of data and materials

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Competing interests

We declare that we have no competing financial interests.

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