

Original Research

Genetic Evaluation and Breeding Strategies under Water Deficit Environment to Develop the Drought Tolerant Wheat Germplasm

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Received: 23 February 2024

Accepted: 27 April 2024

Abstract

Wheat stands out as the most extensively cultivated cereal crop and serves as a primary food source across numerous regions worldwide. Therefore, to assess wheat breeding material for sustained food security, an experiment was carried out. The research material comprised 44 genotypes, encompassing 8 lines, 4 testers, and 32 F₁ generations utilized for the assessment of various indices, including plant height (PH), flag leaf area (FLA), spikelet per spike (SPS), grain per spike (GPS), spike length (SL), 1000-grain weight (TGW), tillers per plant (TP), grain yield per plant (GYP), biological yield per plant (BYP), harvest index (HI), and relative water content (RWC). The data obtained from the studied attributes underwent an analysis of variance to discern significant differences among the lines and testers for each evaluated trait. The results revealed notable variations, indicating the significance of both genetic factors and environmental conditions on trait expression. Among the evaluated traits, Line (L3) and Tester (T2) consistently demonstrated the genotypes exhibiting good combining ability for both general combining ability (GCA) and specific combining ability (SCA). Such favorable combining ability suggests that the offspring resulting from crosses involving Line L3 and tester T2 are likely to inherit desirable traits for drought tolerance. Particularly, the cross between Line L3 and tester T2 mentioned exceptional performance in most of the studied traits and proved to be a promising combination for

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withstanding drought conditions. The observed variations in the performance of different lines and testers under different environments emphasize the importance of selecting genotypes with adaptive traits for specific conditions. By examining dominant and additive gene action, researchers can better understand the genetic basis of drought tolerance in wheat. Consequently, the recommendation is to enhance the production of the varieties that are superior performers with improved attributes by focusing on selection in later (F_3 - F_5) segregating generations in the wheat breeding program.

Keywords: wheat, GCA, SCA, dominant, additive variance, gene-action

Introduction

The wheat crop (*Triticum aestivum* L.) is one of the most important cereal crops worldwide, in terms of production and utilization. Wheat is a major food source, particularly in Pakistan and various parts of the world [1]. Spring wheat (*Triticum aestivum* L.) is a crucial cornerstone food for a significant proportion of the global population, contributing to a vast variety of bakery items. Nevertheless, the exponential rise in Pakistan's population poses a considerable challenge for scientists in the field of agriculture. Addressing the escalating population demands in Pakistan requires urgent efforts toward developing high-yielding wheat varieties by amalgamating favorable traits from existing wheat germplasm into a singular genotype [2].

Significant enhancement in production stands as an urgent imperative, not solely to meet the ever-expanding demand for food within the country for domestic usage but also to facilitate exports, thereby bolstering foreign exchange earnings. Anticipating the burgeoning population, the nation is projected to require approximately 100 million metric tons of wheat by 2030. Achieving this ambitious target demands a consistent increase in wheat production at a rate of 1% per year. This momentous goal can be achieved through two fundamental approaches: horizontal expansion involving the augmentation of cultivated land area and vertical enhancement encompassing hybrid improvement. The latter, in particular, serves as a potent tool capable of effecting substantial leaps in production and across diverging agro-climatic conditions [3, 4].

The selection of suitable genotypes for enhancing crop yield under water scarcity is pivotal for the success of the entire program. In hybrid breeding, a significant hurdle lies in identifying the most optimal parents and combinations among the numerous possibilities to generate the most high performing hybrids [5]. In hybrid breeding, a key challenge often revolves around precisely determining the most suitable parental lines and combinations. This hurdle encompasses factors such as genetic compatibility, heterosis expression, and desirable trait complementation, which collectively influence the success of hybridization programs [1, 6]. In the majority of agricultural breeding initiatives, the primary objectives involve identifying the top successful strains suitable for launching in the field for farmers and discerning lines that hold potential as

parents for future crosses. Certain mating designs, like North Carolina (NC), designs I, II, and III, line \times tester, and diallel can be used to choose the parental line. These designs allow one to distinguish between additive and non-additive genetic contributions within a line [7]. Initially, combining ability was a broad concept employed to categorize an inbred line based on its performance in crosses. The concepts of general combining ability (GCA) and specific combining ability (SCA) have significantly impacted the assessment of inbred lines and the development of populations in crop breeding [8]. The scientist initially described general combining ability (GCA) as the standard performance of a genotype across different hybrid combinations. In contrast, they defined specific combining ability (SCA) as situations where particular hybrid combinations demonstrated either superior or inferior performance compared to what could be predicted based on the average performance of the parental inbred lines. Conversely, if their effectiveness in combining well is limited to certain crosses, the analysis of combining ability is utilized to assess how genotypes perform in diverse cross combinations. The process of figuring out how different yield and quality traits appear depends on the type and degree of gene significance [1, 6, 9, 10].

Numerous studies have delved into the examination of the combining ability and genetic composition of hybrid populations in bread wheat. The selection of best-performing genotypes and their cross combination is necessary for creating desirable wheat varieties. They utilized the line \times tester method to explore traits associated with yield and its components. The findings from the researcher suggest that non-additive gene effects play a significant role in influencing grain yield, plant¹, and various other related traits [11]. In the case of wheat, the effects of both general combining ability (GCA) and specific combining ability (SCA) were significantly noteworthy for all traits, except spike length. The statistical analysis mentioned significant MSS for both GCA and SCA across all the studied traits [1, 10]. The findings indicated that a significant portion of the genetic variance associated with grain yield and its components was predominantly influenced by the additive nature of genes [12]. These assessments aim to shape a more efficient and productive breeding approach, facilitating swift enhancements in this crop. This investigation aimed to acquire insights into the extent of combining ability concerning grain yield

and its associated traits during the selection process. The objectives encompassed identifying promising parent combinations for future breeding programs, estimating genetic parameters like heritability and genetic advances, and discerning both general combining ability (GCA) and specific combining ability (SCA) among different genotypes.

Material and Methods

The research was carried out in the Department of Plant Breeding and Genetics (PBG) research block at the Islamia University of Bahawalpur, Punjab, Pakistan. In this experiment, 32 parents, 4 testers, and 8 lines, a total of 44 genotypes were grown to evaluate yield and yield-related traits by using a randomized complete block design (RCBD) under drought and normal conditions at maturity level. Initially, 10 seeds of each genotype were sown in rows with a distance of 6 inches between the plants and a distance of 12 inches between the rows. After germination, thinning was done, and three plants were selected from each genotype. In the normal experiment, recommended irrigation was applied at three critical stages, i.e., at (1) tillering (35 days after sowing, DAS), (2) booting (85 DAS), and (3) milking (112 DAS; [9]). In the stressed experiment, drought stress was applied at the tillering stage by upholding (missing) the irrigation treatment. One set of genotypes was irrigated at all three critical stages, while the other set of the same wheat genotype was kept under drought stress, missing the irrigation at the first (tillering) critical stage at 35 DAS. During the growing season, all cultural practices were followed as per recommendation. When the plants reached the maturity, data was collected from the eight monitored plants for each genotype under normal and water stressed conditions. The study traits were Plant height (cm), Flag leaf Area (cm²), Spikelet per Spike, Grains per Spike, 1000 grain weight (g), Tillers per plant, Grain yield per plant, Biological Yield/Plant, Harvest Index, and Relative Water Content.

The data underwent Analysis of variance (ANOVA) as given by Steel [13] for different morphological and biochemical traits. The traits exhibiting significant differences were further analyzed by using the line \times tester technique as deliberated by Kempthorne [14]. Through the application of line \times tester analysis on the F₁ generation, encompassing general combining ability and specific combining ability, as well as the determination of gene action type. The formula provided below was employed for the estimation of the combining ability given by Singh [15].

Results and Discussion

The aim of this study was to conduct a genetic evaluation and implement breeding strategies under water deficit conditions to develop drought-tolerant wheat germplasm. By subjecting diverse wheat genotypes to controlled water deficit environments, we sought to assess their performance and identify promising candidates for further breeding efforts. In this section, we present the results of our experiments and discuss their implications for breeding resilient wheat varieties capable of withstanding drought stress. This experiment was carried out for 10 traits for the estimation of the Analysis of variance (ANOVA) for assessing the importance of distinction among the treatments. The (MSS) mean sum of squares for observed traits like Plant height (cm), Flag leaf Area (cm²), Spikelet per Spike, Grains per Spike, 1000 grain weight (g), Tillers per plant, Grain yield per plant, Biological Yield/Plant, Harvest Index, and Relative water Content under normal as well as drought stress conditions presented in Table 1 (under normal conditions) and Table 2 (under drought stress conditions) showed that significant variations were present among all the attributes, while the mean square of testers for TGW and RWC had a non-significant difference under

Table 1. Analysis of variances through L \times T for studied traits under normal conditions.

Traits	PH	FLA	NSS	NGS	TGW	NTP	GYP	BYP	HI	RWC
Replication	15.24*	13.74*	0.54 ^{ns}	3.46*	9.02*	42.48*	51.72*	47.70*	31.24*	12.86 ^{ns}
Genotypes	51.95*	64.45*	19.30*	18.99*	29.49*	31.01*	25.94*	72.56*	20.26*	112.85*
Parents	43.05*	49.89*	32.43*	32.43*	17.70*	14.36*	4.82*	73.82*	38.43*	136.61*
Crosses	22.72*	11.12*	7.38*	7.08*	16.74*	7.17*	9.58*	7.77*	13.58*	13.48*
P. vs C	1055.95*	1878.16*	244.09*	240.34*	554.46*	953.19*	765.5*	2067.22*	27.12*	2931.85*
Lines	31.19*	19.50*	4.98*	6.93*	33.38*	11.56*	6.54*	11.83*	5.70*	19.28*
Testers	5.02*	22.21*	3.37*	5.32*	1.27 ^{ns}	7.01*	6.25*	8.60*	13.43*	2.71 ^{ns}
L \times T	22.42*	6.74*	8.76*	7.38*	13.41*	5.73*	11.07*	6.30*	16.23*	13.08*
Error	1.11	0.70	0.34	0.44	0.68	1.03	0.74	0.40	0.57	4.94
Total	18.01	21.83	6.56	6.58	10.27	11.51	9.79	24.81	7.50	40.48

Table 2. Analysis of variances through L × T for studied traits under drought conditions.

Traits	PH	FLA	NSS	NGS	TGW	NTP	GYP	BYP	HI	RWC
Replication	18.76*	17.31*	1.50*	11.88*	21.48*	25.05*	41.21*	68.22*	7.53*	14.44*
Genotypes	130.40*	98.49*	44.07*	52.55*	15.07*	13.19*	62.80*	38.24*	113.23*	78.60*
Parents	100.43*	68.09*	27.34*	36.56*	14.49*	10.98*	59.70*	72.76*	136.61*	72.45*
Crosses	6.59*	8.71*	5.39*	4.45*	3.97*	5.29*	3.70*	13.61*	7.94*	11.32*
P. vs C	4298.29*	3216.36*	1427.23*	1719.5*	365.73*	282.68*	1929.10*	422.09*	3120.18*	2232.07*
Lines	2.62*	5.15*	2.85*	2.40*	4.80*	4.59*	6.17*	8.48*	4.50*	4.95*
Testers	5.90*	3.00*	3.86*	3.11*	0.87*	2.54*	4.69*	17.24*	12.50*	9.59*
L x T	8.01*	10.71*	6.45*	5.32*	4.13*	5.91*	2.73*	14.79*	8.43*	13.69*
Error	0.54	0.55	0.34	0.27	0.09	0.28	0.58	0.59	1.09	0.62
Total	43.45	32.95	14.71	17.60	5.33	4.90	21.62	13.98	38.00	26.43

(PH) Plant height (cm), (FLA)Flag leaf Area (cm²), (NSS) Spikelet per Spike, (NGP) Grains per Spike, (TGW)1000 grain weight (g), (NTP) Tillers per plant, (GYP) rain yield per plant, (BYP) Biological Yield/Plant, (HI) Harvest Index, (RWC) Relative water Content

normal conditions. Mean variability and combining ability effects of parents and crosses under normal and water stress conditions for each trait are given below.

Plant Height

Among 12 parents, the average performance was noted among (T4) 89.5 cm to (L3) 103.5cm under normal

conditions as presented in Fig. 1A, while mean values ranged from (T3) 61.50cm to (L3) 78.50 cm under water stress conditions, as displayed in Fig. 1B. Among F₁ hybrids under normal conditions, the range varied from 98.17 cm (L6 × T2) to 109.5 cm (L3 × T2), as depicted in Fig. 2, whereas the mean performance under water stress conditions ranged from 79.50 cm (L4 × T3) to 84.50 cm (L3 × T2), as displayed in Fig. 2.

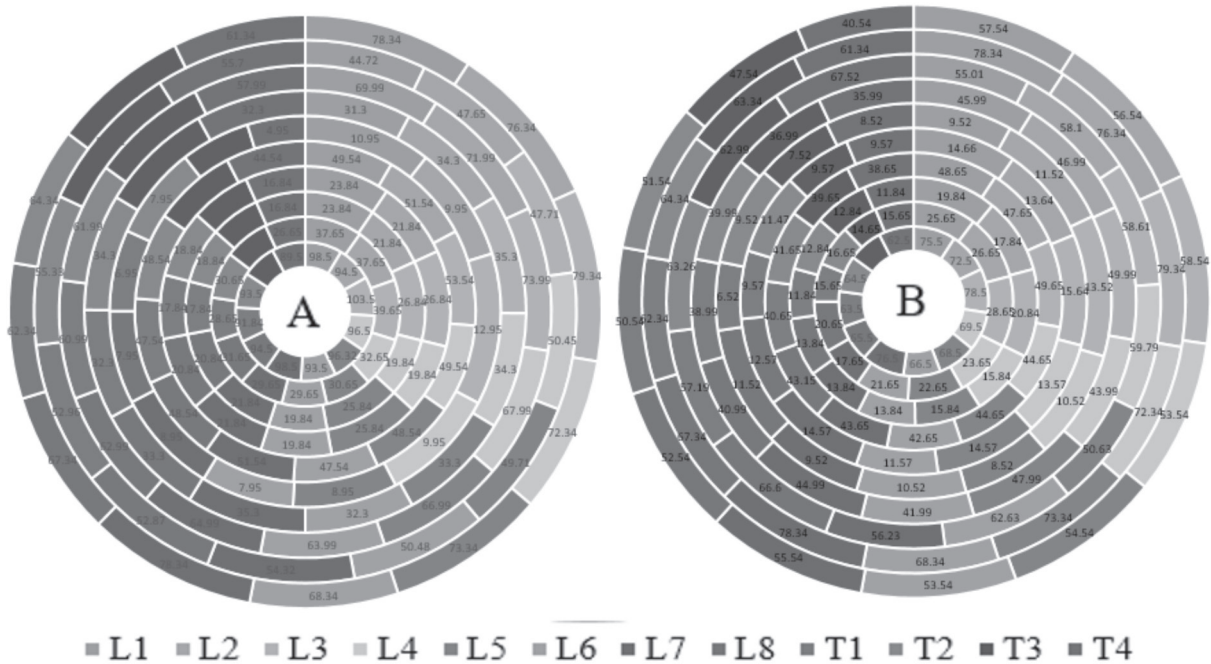


Fig. 1. Mean performance of parents (Lines and Testers) under normal (A) and Drought (B) conditions.

In these fig. the inner first ring for (PH) Plant height (cm) followed by (FLA)Flag leaf Area (cm²), (NSS) Spikelet per Spike, (NGP) Grains per Spike, (TGW)1000 grain weight (g), (NTP) Tillers per plant, (GYP) rain yield per plant, (BYP) Biological Yield/Plant, (HI) Harvest Index and last outer ring for (RWC) Relative water Content trait.

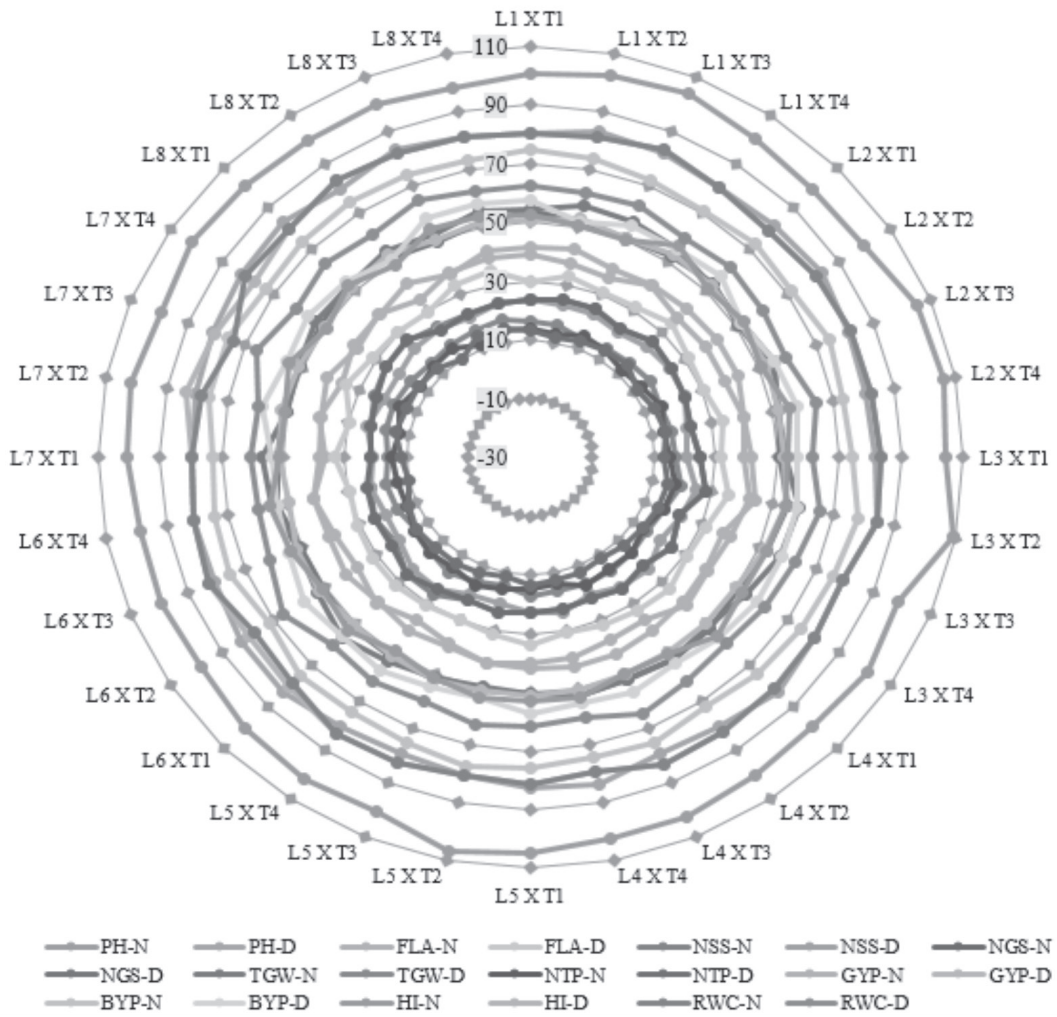


Fig. 2. Mean performance of crosses under normal and drought conditions.

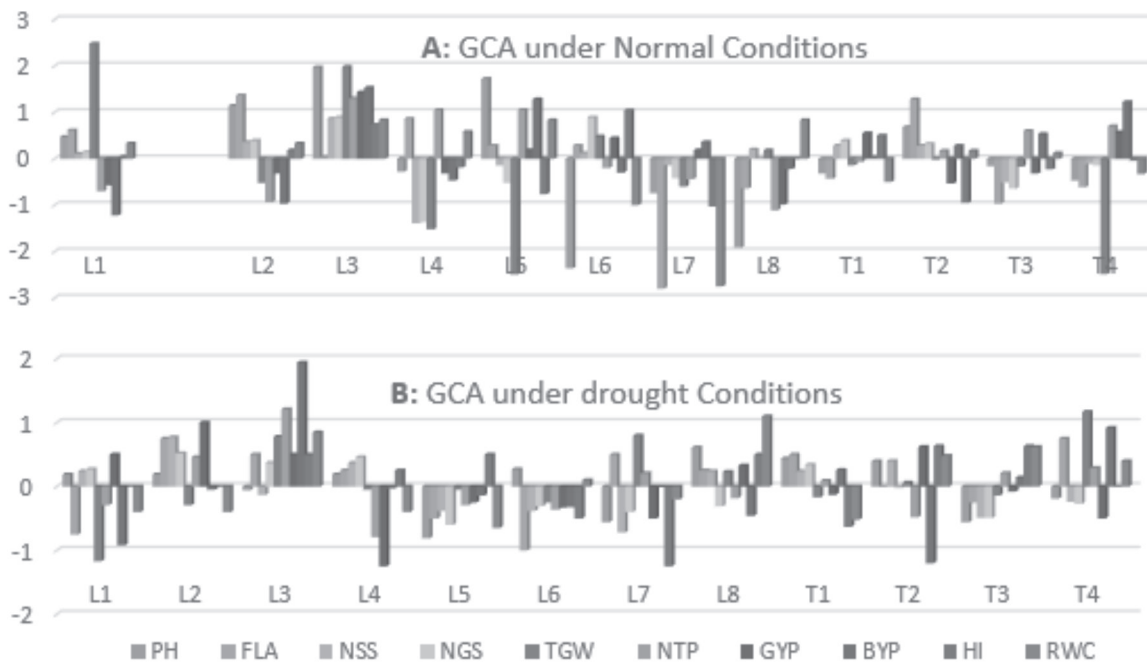


Fig. 3. General combining ability of lines and testers under normal (A) and drought (B) condition.

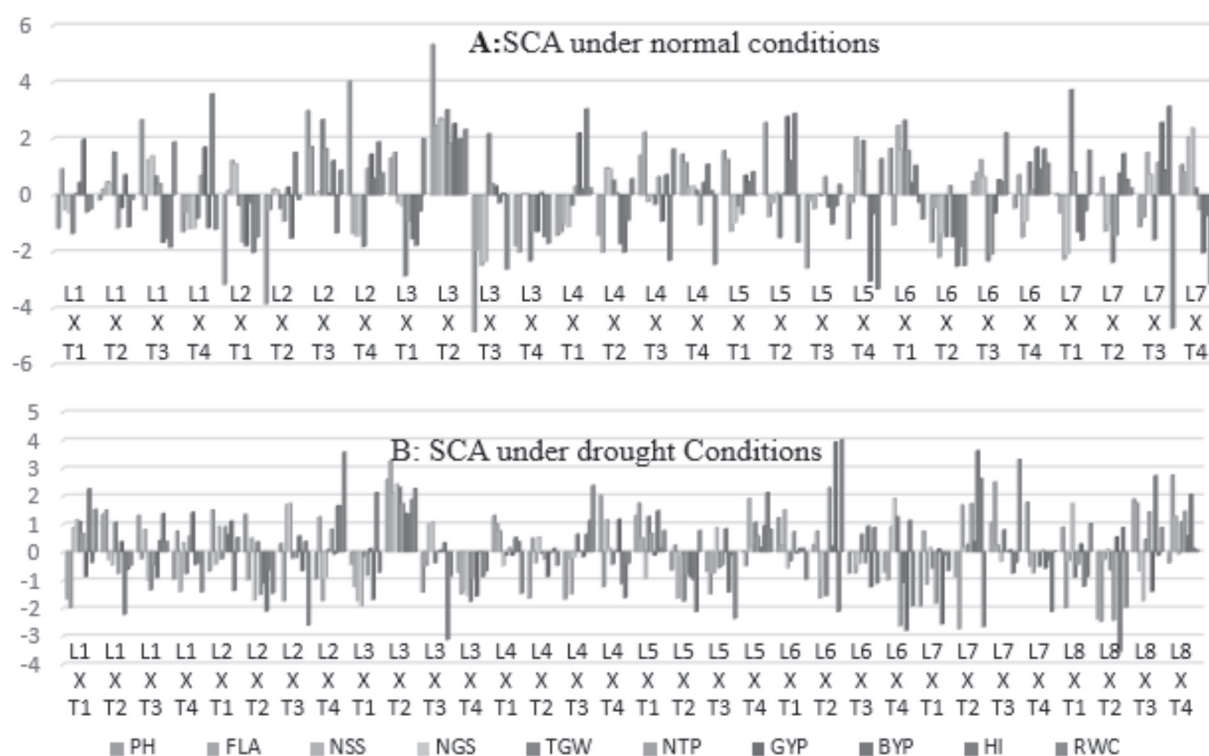


Fig. 4. Specific combining ability of crosses under normal (A) and drought (B) conditions.

In the F_1 generation, SCA effects for this trait ranged from -4.84 ($L3 \times T3$) to 5.32 ($L3 \times T2$) in non-stressed circumstances, and amidst water stress conditions, SCA effects for this trait ranged from -2.39 ($L8 \times T2$) to 2.60 ($L3 \times T2$). There were notable and favorable effects concerning specific combining ability obtained for five crosses under normal conditions and for ten crosses under water stress conditions. Under normal and water stressed conditions, the cross ($L3 \times T2$) showed significant and positive SCA effects and proved to be good general combiners Fig. 4A and B.

Flag Leaf Area

Among parents, the average performance ranged between 26.64 (T4) and 39.64 (L3) for this parameter under normal conditions as presented in Fig. 1A, while the mean performance ranged from 14.65 (T3) to 28.65 (L3) for this attribute under water stress conditions, as shown in Fig. 1B. Among 32 crosses, the average value varied from 35.97 ($L7 \times T3$) to 44.31 ($L3 \times T2$) under normal conditions as given in Fig. 2. The minimum flag leaf area in F_1 was found to be 29.65 ($L6 \times T4$) to 35.65 ($L3 \times T2$) under water stress conditions, as exhibited in Fig. 2.

Among the lines, L1 showed a significant GCA effect in the preferred outcome under normal conditions, while lines L1 and L6 under water stress conditions reflected positive and significant GCA effects. Among testers, all the testers under normal and water stressed conditions T2 were observed to be good general combiners, as shown in Fig. 3A and B, respectively. For flag leaf

weight, the range of the SCA effect was observed from -2.03 ($L3 \times T4$) to 2.47 ($L3 \times T2$) under normal conditions and from -2.75 ($L7 \times T2$) to 3.45 ($L3 \times T2$) under water stress conditions. In general, five crosses ($L2 \times T3$), ($L3 \times T1$), ($L3 \times T2$), ($L4 \times T3$), and ($L8 \times T4$) in normal conditions and eight crosses ($L1 \times T2$), ($L2 \times T1$), ($L2 \times T4$), ($L3 \times T2$), ($L5 \times T1$), ($L7 \times T3$), ($L8 \times T3$), and ($L8 \times T4$) under water stress conditions had significantly positive SCA effects, as exhibited in Fig. 4A and B, respectively.

Number of Spikelets per Spike

The genotypes that possess a higher number of spikelets per spike are selected, which leads to higher wheat grain yield production. Among 12 parents, average performance among the genotypes was observed with values of 16.83 (T3, T4) to 26.83 (L3) for this parameter under normal conditions as presented in Fig. 1A, while the average performance varied from 11.84 (T4) to 20.84 (L3) under water stress conditions for this specific trait as displayed in Fig. 1B. Among crosses, the mean values varied from 21.83 ($L3 \times T3$, $L4 \times T1$, $L4 \times T3$, $L7 \times T1$) to 27.83 ($L3 \times T2$) for this trait under normal conditions (Fig. 2). The mean performance range in F_1 progenies was observed from 20.84 ($L7 \times T1$) to 24.84 ($L3 \times T2$) for this trait under water stress conditions, as exhibited in Fig. 2.

Among the lines, L3 under normal conditions was found to be positive and significant and demonstrated to be a good general combiner, whereas under water stress conditions, lines L1 and L4 were found to be

significantly superior general combiners. Among testers under normal and water stress conditions, T2 was found to be a promising general combiner, as exhibited in Fig. 3A and B, respectively. On the basis of SCA effects under normal conditions, the best three crosses for this character were (L3×T2), (L6× T1), and (L7× T4) whereas under water stress conditions, the best three crosses were (L3× T2), (L5× T4), and (L2× T3), as exhibited in Fig. 4A and B.

Number of Grains per Spike

For this trait among 12 parents, average performance was between 16.84 (T4) to 26.84 (L3) under normal conditions as presented in Fig. 1 A, while the values of mean performance ranged from 38.65 (T4) to 49.65 (L3) for this trait under water stress conditions as displayed in Fig. 1 B. Among 32 crosses, the average value ranged from 21.83 (L7 × T1) to 27.83 (L3 × T2) for this trait under normal conditions, as displayed in Fig. 2. The mean performance range in F_1 progenies was found to be from 49.33 (L8 × T3) to 54.65 (L3 × T2) for the specific attribute of under water stress conditions, as exhibited in Fig. 2.

Under both conditions, the lines L1 and L3 showed significantly desirable GCA effects, whereas the tester T2 was observed as a good general combiner under normal conditions, while no cross performed as a positive significant general combiner under water stress conditions depicted in Fig. 3A and B. The range of the SCA effect was observed from -2.36 (L3 × T3) to 2.68 (L3 × T2) under normal conditions and from -1.94 (L3 × T1) to 2.42 (L3 × T2) under water stress conditions. Six cross combinations in normal and eight in water stress conditions showed significant and positive SCA effects for this character, as depicted in Fig. 4A and B.

1000-Grain Weight

Thousand grain wheat can be a significant trait influencing yield and could be used as a parameter for selection to achieve more wheat production. Amid nine parents, the mean values were between 44.54 g (T4) and 53.54 g (L3) for this parameter under normal conditions, as presented in Fig. 1 A, while mean performance ranged from 9.57 g (T4) to 15.64 g (L3) for this trait under water stress conditions, as displayed in Fig. 1B. Among the resulting crosses, average values ranged from 49.53 g (L5× T2) to 58.53 g (L3× T2) for this trait under normal conditions, as shown in Fig. 2, whereas average variations in crosses under water stress conditions were found to be between 13.65 g (L1× T3) and 19.47 g (L3× T2) for this character, as presented in Fig. 2.

Testers T2 and T4 exhibited positive GCA effects under water stress conditions. However, among lines, the L3 showed the most desirable GCA effects under both conditions and thus was found to be a good combiner for this trait (Fig. 3 A and B). For this character, the range of the SCA effect under normal conditions was observed

from -2.86 (L3 × T1) to 3.73 (L7 × T1), whereas under water stress conditions this range varied between -1.77 (L3 × T4) and 2.31 (L3 × T2). Nine crosses amid water stress conditions had significantly positive SCA effects, while eight crosses had significantly positive SCA effects under normal conditions. Under water stress conditions among these nine crosses, the superior performing three in order of merit were (L3× T2), (L6× T4), and (L3× T2) for this trait (Fig. 4A and B).

Number of Tillers per Plant

Amidst 12 parents, the number of tillers' mean performance varied between 4.95 (T4) and 12.95 (L3) for this parameter under normal conditions, as presented in Fig. 1A, while the average range of values was from 6.52 (T1) to 13.52 (L3) for attribute under water stress environments, as displayed in Fig. 1B. Among F_1 hybrids, the range varied from 11.31 (L8× T3) to 17.95 (L3 × T2) for this trait under normal conditions (Fig. 2). The mean performance range in F_1 generation was found to be from 9.95 (L8 × T2) to 15.52 (L3 × T2) under water stress conditions for this trait, as displayed in Fig. 2.

The number of tillers per plant exhibited positive and significant General Combining Ability (GCA) effects. Specifically, lines L3 and L4 displayed positive and significant GCA effects under normal conditions, while Line L3 was positive and significant under water stress conditions. The line L3 with the T2 and T3 proved to be good general combiners in order of merit under normal and water stress conditions, as displayed in Fig. 3 A and B. Two cross combinations under normal conditions and six crosses under water stress conditions showed positive and significant SCA effects for this character. When considering SCA effects, the top crosses for this trait were (L2 × T3) and (L3 × T2) under normal conditions, whereas under water stress conditions, the best six crosses were (L2× T1), (L3× T2), (L6× T2), (L7× T2), (L8× T3), and (L8× T4), as exhibited in Fig. 4A and B.

Grain Yield per Plant

The average performance was observed between 31.30 (L1) and 35.30 (L3) between 12 parents for this trait under normal conditions, as presented in Fig. 1A while the average performance values varied from 35.99 (T4) to 49.99 (L3) under water stress condition for this specific trait, as displayed in Fig. 2. Among 32 crosses, the mean value varied from 34.62 (L8 × T2) to 42.30 (L3 × T2) for this trait under normal conditions. The mean performance range in F_1 progenies was found to be 49.66 (L6 × T4) to 53.99 (L3 × T2) for this character under water stress conditions, as exhibited in Fig. 2.

Among parents, line L3 under normal and water stress conditions was found to be a good general combiner. Among testers, T1 showed desirable GCA

effects under normal and T4 under water stress conditions, as shown in Fig. 3A and B. Seven cross combinations in normal conditions and two crosses in water stress conditions showed positive and significant SCA effects for this character. On the basis of SCA effects, the best two crosses for this character were (L5 × T2) and (L7 × T3) under normal conditions, whereas the best crosses on the basis of SCA effects under water stress conditions were (L3 × T2) and (L1 × T4), as exhibited in Fig. 4A and B.

Biological Yield per Plant

Among 12 parents, the variation was between 57.99 (T4) and 73.99 (L3) for this parameter under normal conditions, as presented in Fig. 1A, while mean values ranged from 50.63 (L5) to 67.52 (T4) for this trait under water stress conditions, as displayed in Fig. 1B. Among F_1 hybrids, the range varied from 71.66 (L6 × T2) to 77.99 (L3 × T2) for this trait under normal conditions, as shown in Fig. 2. The mean performance in F_1 generation under water stress conditions ranged from 50.65 (L8 × T2) to 58.61 (L3 × T4) for this character, as displayed in Fig. 2.

For this trait, under normal conditions, testers T2 and T3, and under water stress conditions, the testers T3 and T4 showed significantly desirable GCA effects. Among lines, L3 under normal and water stress conditions was observed as a good general combiner for this trait, as shown in Fig. 3 A and B. In F_1 generation, SCA effects for this trait ranged from -2.52 (L6 × T2) to 1.97 (L3 × T2) under normal conditions, while this range varied between -3.57 (L8 × T2) and 3.97 (L6 × T2) under water stress conditions. Desired and significant SCA effects were obtained for seven crosses under normal and eight crosses under water stress conditions. However, the best three crosses in order of merit were (L1 × T1), (L3 × T2), and (L7 × T2) under normal conditions, while under water stress conditions, the three best crosses in order of merit were (L1 × T1), (L2 × T4), and (L3 × T2) (Fig. 4A and B).

Harvest Index

Among 12 parents, the mean values were between 44.72 (L1) and 55.70 (T4) for this parameter under normal conditions, as presented in Fig. 1A, while mean performance ranged from 61.34 (T4) to 79.34 (L3) for this trait under water stress conditions, as displayed in Fig. 1B. Among the resulting crosses, the mean values ranged from 48.41 (L8 × T2) to 55.82 (L4 × T1) (L6 × T1) for this trait under normal conditions, as depicted in Fig. 2. The mean value under water stress conditions in crosses was found to be between 77.34 (L7 × T4) and 84.34 (L4 × T1) (L6 × T1) for this character, as presented in Fig. 2.

Under both conditions, L3 showed significant GCA effects, whereas the tester T3 under normal conditions was observed as a good general combiner, as depicted

in Fig. 3A and B. For this character, the range of the SCA effect was observed from -1.85 (L1 × T3) to (L1 × T4) under normal conditions, whereas this range varied between -3.13 (L3 × T3) and 2.63 (L7 × T3) under water stress conditions, as depicted in Fig. 3A and B. Nine crosses were under normal conditions, while under water stress conditions five crosses had significantly positive SCA effects. Out of these crosses under normal conditions, the top three for this trait in order of merit were (L1 × T4), (L2 × T2), and (L3 × T2) while under water stress environments, the best three crosses for this trait in order of merit were (L7 × T3), (L3 × T1), and (L3 × T2), as exhibited in Fig. 4 A and B, respectively.

Relative Water Content

Among 12 parents, the mean values were between 61.34 (T4) and 79.34 (L3) for this parameter under normal conditions, as presented in Fig. 1A, while mean performance ranged from 40.54 (T4) to 58.54 (L3) for this trait under water stress conditions, as displayed in Fig. 1B. Among the resulting crosses, the mean values range from 73.66 (L7 × T3) to 84.34 (L3 × T2) for this trait under normal conditions, as depicted in Fig. 2. The mean value under water stress conditions in crosses was found between 59.54 (L6 × T4) and 64.54 (L6 × T2) for this character, as presented in Fig. 2.

L3 showed significant GCA effects under both conditions, whereas the tester T2 and T3 under normal conditions and testers T2 and T4 under water stress conditions was observed as a good general combiner, as depicted in Fig. 3 A and B. For this character, the range of the SCA effect was observed from -2.86 (L2 × T3) to 3.48 (L3 × T2) under normal conditions, whereas this range varied between -1.16 (L5 × T4) and 1.78 (L3 × T2) under water stress conditions, as depicted Fig. 3A and B. Two crosses under normal conditions and six crosses under water stress conditions had significantly positive SCA effects. Out of these crosses under normal conditions, the best for this trait in order of merit were (L7 × T3) and (L7 × T4), while under water stress environments, the best three crosses for this trait in order of merit were (L1 × T1), (L2 × T4), and (L4 × T3), as exhibited in Fig. 4A and B, respectively.

Genetic Evaluation

The analysis was conducted for the estimation of the genetic component of variance, specifically focusing on the variance attributable to general combining ability (σ^2_g) and specific combining ability (σ^2_s) for both attributes studied under normal and water stress conditions. The results presented in Table 3 revealed that the genetic variances with GCA and SCA in both environments primarily emphasized the dominance of specific combining ability, indicating the influence of non-additive genetic effects on the expression of all the studied attributes. However, it is worth noting that the

Table 3. Genetic evaluation of Parents and Crosses Under Both Conditions.

Plant traits	Gene action				Contribution of parents and their crosses					
	Additive		Dominance		Line		Tester		L×T	
	N	WD	N	WD	N	WD	N	WD	N	WD
Plant height	0.01	-0.05	7.11	2.49	31	9	2	9	67	82
Flag leaf Area	0.15	-0.07	2.01	3.39	40	13	19	3	41	83
Spikelet per Spike	-0.05	-0.04	2.81	2.04	15	12	4	7	80	81
Grains per Spike	-0.01	-0.03	2.31	1.69	22	12	7	7	71	81
1000 grain weight	0.11	-0.01	4.24	1.35	45	27	1	2	54	71
Tillers per plant	0.05	-0.02	1.57	1.88	36	20	9	5	54	76
Grain yield per plant	-0.05	0.03	3.44	0.72	15	38	6	12	78	50
Biological Yield/Plant	0.05	-0.04	1.97	4.74	34	14	11	12	55	74
Harvest Index	-0.09	-0.02	5.22	2.45	9	13	10	15	81	72
Relative water Content	0.01	-0.08	2.71	4.60	32	10	2	8	66	82

number of grains per spike exhibited an additive genetic action under both conditions (Table 3).

The investigation of the study analyzed the influence of both dominance and additive genetic action on several yield related attributes under normal and water stress conditions. Focusing on the traits, such as flag leaf area, thousand-grain weight, biological yield per plant, plant height, number of spikes per plant, spikelet per spike, spike length, spike density, grain yield per plant, and harvest index, these specific studies showed non-additive genetic effects. To determine the relative contribution of interaction between line × tester to the overall variance across various plant characters, a line × tester study of eight lines and four testers was conducted and adjusted as presented in Table 3. Amidst observing the proportional contribution of female parents (lines), male parents (testers), and their hybrids to the total variance for studied traits, the most prominent among all were lines for characters like plant height, spike length, spike density, number of grains per spike, 1000-grain weight, biological yield per plant, grain yield per plant, and harvest index under normal and water stress conditions, indicating a predominant maternal influence. The contribution of male parents (testers) was very low in proportion to most of the studied traits under both conditions. While observing the proportional contribution of female parents (lines), male parents (testers), and their hybrids to the total variance for studied traits, lines were more prominent for characters like plant height, spike length, spike density, number of grains per spike, 1000-grain weight, biological yield per plant, grain yield per plant, and harvest index under normal and water stress conditions, indicating a predominant maternal influence. The contribution of male parents (testers) was very low in proportion to most of the studied traits under both conditions.

Discussion

The desired variations are indicated by significant results, while the non-significant results showed undesirable variations that are not useful for plant breeders for further genetic studies. Many researchers reported significant variations among yield related traits [16-19]. Among hybrids, the presence of variability is of utmost significance in the development and improvement of wheat for water deficit tolerance.

In wheat breeding programs, the plant height character is a key parameter. Plant breeders tend to choose compact or shorter genotype selections in areas prone to lodging, whereas they prefer taller cultivars for regions characterized by water stress [20]. It is preferable in wheat to have a short plant stature because plants with greater height have more lodging issues and require more input and energy to transport photosynthates to the grains in wheat [21]. An optimal plant height is linked to lower chances of lodging, a higher grain count per spike, and a better harvest index, resulting in improved grain yield and quality [22]. The size of the flag leaf is crucial as it contributes significantly to the photosynthesis process. Similar research indicated that as a reaction to the water stressed environment, all the cultivars showed a decrease in leaf succulence, stomatal opening area, shoot biomass, density, and distribution, but to varying extents [23]. Similar results were also reported [24] for the number of spikelets per spike, indicating that drought stress can reduce the number of spikelets, affecting the development and fertility of crops such as rice and barley. These circumstances can lead to a decrease in grain yield and quality under drought conditions. The number of grains per spike stands as a crucial trait that affects the yield of the wheat and directly influences the genotype's yield potential. Consequently, plant breeders aim for the development

of new wheat genotypes with a higher number of grains per spike. Thus, it can be considered a key parameter for the selection and development of new wheat cultivars. The results showed drought stress can have a negative effect on the number of grains in wheat by causing pollen and spikelet abortion, reduced grain filling, and lower grain weight. Similar results were reported in previous studies [25, 26]. The results showed that drought stress can have an adverse impact on the thousand grain weight of wheat by reducing grain filling, grain size, and kernel hardness. The effect of drought on wheat thousand grain weight and quality depends on duration, timing, and the impact of the stress, as well as the wheat genotype and growing conditions [27, 28]. The number of tillers per plant is an important factor for crop yield and biomass production. [29, 30] reported that drought stress has a negative effect on the number of tillers per plant in different crop plants such as rice, wheat, and barley by reducing growth and photosynthesis processes. Similar results were observed in this research. A multifaceted characteristic is grain yield; the primary focus of plant breeders lies in the development of high yielding cultivars to meet the demands of the food industry in the country. Their efforts aim to improve this specified trait, either directly or indirectly. Variations between the genotypes for yield related traits and grains concerning wheat are the most important attributes in wheat plant breeding programs [31]. The total dry matter produced by a crop plant is called biological yield, which includes both economic and non-economic parts. Biological yield is an important indicator of crop productivity and resource use efficiency [32]. According to the research results, drought stress can have a negative effect on the biological yield of crop plants such as wheat and rice by reducing plant biomass, water use efficiency, photosynthesis, and nutrient uptake. Similar results were reported [33, 34]. The proportion of grain yield relative to the total biomass of grain, leaves, and stems represents the Harvest index (HI). Environmental factors, such as water availability, can influence HI. Drought stress occurring during the flowering and filling stages has the most significant impact on the Harvest index [35]. RWC can be used as an indicator of drought tolerance in plants, as higher RWC reflects better osmotic regulation or lower elasticity of the tissue cell wall. The results showed that RWC is affected by drought stress, which reduces water availability and causes dehydration of plant cells. Drought stress also reduces the growth, yield, and photosynthesis of plants, similar results were reported [36, 37].

For plant height, significant and positive SCA effects were obtained, which mean this trait was affected by dominance gene action and proved to be good general combiners under both conditions. Similar results were reported by several wheat scientists [38]. The flag leaf area reported a high effect of SCA variance. This attribute also exhibited dominant gene action as a good combiner. Experiments on this trait with the same results were conducted and reported in previous studies

[39]. Eight cross combinations under normal and water stress conditions exhibited positive and significant SCA effects for the number of spikelets per spike. These results are in agreement with the findings of previous studies [30, 40] for the number of spikelets per spike. Under both conditions, lines L1 and L3 showed significantly desirable GCA effects for the number of grains per spike, whereas six cross combinations in normal and eight in water stress conditions showed positive and significant SCA effects for this character. Similar results were reported by previous findings made by wheat scientists [30]. Thousand grain weight observed significantly positive GCA effects exhibited by testers T2 and T4 under water stress conditions while L3 under both conditions showed the maximum desirable GCA effects and thus was found to be a good combiner for this trait. These results are in accordance with previous studies [41] for 1000-grain weight. The line L3 and testers T2 and T3 proved to be good general combiners under normal and water stress conditions as they exhibited positive and significant GCA effects, which means additive gene action was more prominent. Significant results were also reported [30] for the number of tillers per plant. On the basis of SCA effects, the best three crosses for this character were (L2 × T3) and (L3 × T2) under normal conditions, whereas under water stress conditions, the best six crosses were (L2 × T1), (L3 × T2), (L6 × T2), (L7 × T2), (L8 × T3), and (L8 × T4). Similar results were reported by various scientists [42]. For the biological yield per plant, under normal conditions, the testers T2 and T3, and under water stress conditions the testers T3 and T4, showed significantly desirable GCA effects. Among lines, L3 under normal and water stress conditions was observed as a good general combiner for this trait. Desired and significant SCA effects were obtained for seven crosses under normal and eight crosses under water stress conditions. Similar results were obtained by wheat breeders [30]. The Harvest index mentioned lines have additive gene action while crosses have more SCA effects, which means crosses had dominant gene action among them. Many scientists [43] have also shown the same results. In the relative water content trait, L3 showed significant GCA effects, whereas testers T2 and T3 under normal conditions and testers T2 and T4 under water stress conditions were observed as good general combiners. Two crosses under normal conditions and six crosses under water stress conditions had significantly positive SCA effects. These results are in agreement with previous wheat breeder studies [40].

Non-additive gene action for traits like plant height, flag leaf area, number of spikes per plant, number of spikelets per spike, spike length, spike density, 1000-grain weight, biological yield per plant, grain yield per plant, and harvest index have been illustrated in these studies. These results are in conformity with the findings of wheat scientists [44], who also observed additive types of gene action for the traits like plant height, flag leaf area, number of spikes per plant,

number of spikelets per spike, 1000-grain weight, and grain yield per plant. Additive types of gene action for the spike length and grain weight per spike have been reported earlier by different plant scientists [38]. While an equal contribution of additive as well as non-additive gene action was reported by wheat breeders [45] in the inheritance of these characters under study, the line \times tester interaction contributed predominantly to flag leaf area, flag leaf weight, number of spikelets per spike, spike length, spike density, 1000-grain weight, grain yield per plant, and harvest index under both conditions. Similar findings were reported by wheat scientists [41].

Conclusions

The results revealed notable variations, indicating the influence of both genetic factors and environmental conditions on trait expression. This interaction underscores the importance of considering both genetic adaptability and the prevailing environmental conditions when selecting wheat genotypes for improved performance under drought stress. On the basis of evaluated traits, Line L3 and tester T2 consistently demonstrated favorable performance in both normal and drought environments. These parental genotypes exhibited good combining ability for both GCA and SCA. Such favorable combining ability suggests that the offspring resulting from crosses involving line L3 and tester T2 are likely to inherit desirable traits for drought tolerance. The observed variations in the performance of different lines and testers under different environments emphasize the importance of selecting genotypes with adaptive traits for specific conditions. By examining dominant and additive types of gene action in this study, researchers can better understand the genetic basis of drought tolerance in wheat. This understanding provides a foundation for targeted breeding efforts aimed at improving drought tolerance and overall yield in wheat crops.

Acknowledgments

All authors thank full of China Agriculture Research System of MOF and MARA (CARS-05-01A-04) Major science and technology projects in Yunnan Province (202102AE090014).

Conflict of Interest

The authors declare no conflict of interest.

References

1. AHMED H. G.M.-D., MUHAMMAD D., KHAN M.A., ULLAH A. Genetic Basis of Physiological and

- Yield Attributes in Spring Wheat for Water-Deficit Environments. *Gesunde Pflanzen*. **74** (4), 1029, **2022**.
2. KHAN M.A., KASHIF M., AHMAD J., KHAN A. S., KHALIQ I., BILQUEES F., SHAUKAT S. SADAF-a potential donor for enhancing frequency of doubled haploids in wheat \times maize crossing system. *Pakistan Journal of Agricultural Sciences*. **51** (2), 353, **2014**.
3. RAJPUT R.S., KANDALKAR V. Combining ability and heterosis for grain yield and its attributing traits in bread wheat (*Triticum aestivum* L.). *Journal of Pharmacognosy and Phytochemistry*. **7** (2), 113, **2018**.
4. IJAZ M., AFZAL A., SHABBIR G., IQBAL J., RAFIQUE M. Breeding wheat for leaf rust resistance: past, present and future. *Asian Journal of Agriculture and Biology*. **2023**.
5. GOWDA M., KLING C., WÜRSCHUM T., LIU W., MAURER H., HAHN V., REIF J. Hybrid breeding in durum wheat: heterosis and combining ability. *Crop Science*. **50** (6), 2224, **2010**.
6. AHAMED H., KHAN A.S., KASHIF M., KHAN S.H. Genetic analysis of yield and physical traits of spring wheat grain. *Journal of the National Science Foundation of Sri Lanka*. **46** (1), 23, **2018**.
7. OAKEY H., VERBYLA A., PITCHFORD W., CULLIS B., KUCHEL H. Joint modeling of additive and non-additive genetic line effects in single field trials. *Theoretical and Applied Genetics*. **113**, 809, **2006**.
8. SPRAGUE G.F., TATUM L.A. General vs. specific combining ability in single crosses of corn. *Journal of the American Society of Agronomy*. **34** (10), **1942**.
9. AHMED H., KHAN A.S., MUHAMMAD K., KHAN S.H. Genetic mechanism of leaf venation and stomatal traits for breeding drought tolerant lines in wheat. *Bangladesh Journal of Botany*. **46** (1), 35, **2017**.
10. AHMED H.-D., KASHIF M., SAJJAD M., ZENG Y.-W. Genetic dissection of protein and gluten contents in wheat (*Triticum aestivum* L.) under normal and drought conditions. *Applied Ecology & Environmental Research*. **18** (4), **2020**.
11. SOYLU S., AKGÜN N. Combining ability and inheritance of some agronomical traits in bread wheat (*Triticum aestivum* L.). *Selcuk Journal of Agriculture and Food Sciences*. **21** (41), 104, **2007**.
12. IQBAL M.M. Combining ability analysis in wheat. *Pakistan Journal of Agricultural Sciences*. **44**, 1, **2007**.
13. STEEL R., TORRIE J., DICKEY 3RD D. McGraw Hill Book Co. New York, NY. **1997**.
14. KEMPTHORNE O. Some aspects of experimental inference. *Journal of the American Statistical Association*. **61** (313), 11, **1966**.
15. SINGH R.K., CHAUDHARY B.D. Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Delhi, India. **1977**.
16. GAO L., MENG C., YI T., XU K., CAO H., ZHANG S., YANG X., ZHAO Y. Genome-wide association study reveals the genetic basis of yield-and quality-related traits in wheat. *BMC Plant Biology*. **21** (1), 1, **2021**.
17. ZHAO J., SUN L., GAO H., HU M., MU L., CHENG X., WANG J., ZHAO Y., LI Q., WANG P. Genome-wide association study of yield-related traits in common wheat (*Triticum aestivum* L.) under normal and drought treatment conditions. *Frontiers in Plant Science*. **13**, 1098560, **2023**.
18. NAGHAVI M.R., MOGHADDAM M., TOORCHI M., SHAKIBA M.R. Evaluation of the relationship between morphological and agronomic traits with grain yield in

- spring wheat cultivars under drought stress. *International Journal of Biosciences*. **5** (3), 88, **2014**.
19. SALMAN S., SHAH J., KHAN J., REHMAT K., KHAN U., KHAN I. Genetic variability studies in bread wheat (*Triticum aestivum* L.) accessions. *Pakistan Journal of Agricultural Research*. **27** (1), **2014**.
 20. BAENZIGER P. Wheat breeding and genetics. Reference Module in Food Science. **1**, **2016**.
 21. ISLAM M.A., OBOUR A.K., SAHA M.C., NACHTMAN J.J., CECIL W.K., BAUMGARTNER R.E. Grain yield, forage yield, and nutritive value of dual-purpose small grains in the Central High Plains of the USA. *Crop Management*. **12** (1), 1, **2013**.
 22. YU M., LIU Z.-H., YANG B., CHEN H., ZHANG H., HOU D.-B. The contribution of photosynthesis traits and plant height components to plant height in wheat at the individual quantitative trait locus level. *Scientific Reports*. **10** (1), 12261, **2020**.
 23. MICKKY B., ALDESUQUY H., ELNAJAR M. Effect of drought on yield of ten wheat cultivars linked with their flag leaf water status, fatty acid profile and shoot vigor at heading. *Physiology and Molecular Biology of Plants*. **26**, 1111, **2020**.
 24. GOL L., HARALDSSON E.B., VON KORFF M. Ppd-H1 integrates drought stress signals to control spike development and flowering time in barley. *Journal of Experimental Botany*. **72** (1), 122, **2021**.
 25. ALI N., AKMAL M. Wheat growth, yield, and quality under water deficit and reduced nitrogen supply. A review. *Gesunde Pflanzen*. **74** (2), 371, **2022**.
 26. VICTORIA O., IDORENYIN U., ASANA M., JIA L., SHUOSHUO L., YANG S., OKOI I.M., PING A., EGRINYA E.A. Seed treatment with 24-epibrassinolide improves wheat germination under salinity stress. *Journal of Applied Biology & Biotechnology*. **10** (4), **2022**.
 27. ZAHRA N., WAHID A., HAFEZ M.B., ULLAH A., SIDDIQUE K.H., FAROOQ M. Grain development in wheat under combined heat and drought stress: Plant responses and management. *Environmental and Experimental Botany*. **188**, 104517, **2021**.
 28. OSTMEYER T., PARKER N., JAENISCH B., ALKOTAMI L., BUSTAMANTE C., JAGADISH S.K. Impacts of heat, drought, and their interaction with nutrients on physiology, grain yield, and quality in field crops. *Plant Physiology Reports*. **25**, 549, **2020**.
 29. ANJUM S.A., ASHRAF U., ZOHAIB A., TANVEER M., NAEEM M., ALI I., TABASSUM T., NAZIR U. Growth and developmental responses of crop plants under drought stress: a review. *Zemdirbyste-Agriculture*. **104** (3), **2017**.
 30. SINGH A., KUMAR A. Gene action analysis for yield and yield contributing traits in bread wheat. *International Journal of Basic and Applied Biology*. **2** (1), 17, **2014**.
 31. THITISAKSAKUL M., JIMÉNEZ R.C., ARIAS M.C., BECKLES D.M. Effects of environmental factors on cereal starch biosynthesis and composition. *Journal of Cereal Science*. **56** (1), 67, **2012**.
 32. KUNDEL D., BODENHAUSEN N., JØRGENSEN H.B., TRUU J., BIRKHOFFER K., HEDLUND K., MÄDER P., FLIESSBACH A. Effects of simulated drought on biological soil quality, microbial diversity and yields under long-term conventional and organic agriculture. *FEMS Microbiology Ecology*. **96** (12), fiae205, **2020**.
 33. DE ALMEIDA G.H.G., DE CÁSSIA SIQUEIRA-SOARES R., MOTA T.R., DE OLIVEIRA D.M., ABRAHÃO J., DE PAIVA FOLETTO-FELIPE M., DOS SANTOS W.D., FERRARESE-FILHO O., MARCHIOSI R. Aluminum oxide nanoparticles affect the cell wall structure and lignin composition slightly altering the soybean growth. *Plant Physiology and Biochemistry*. **159**, 335, **2021**.
 34. DIETZ K.J., ZÖRB C., GEILFUS C.M. Drought and crop yield. *Plant Biology*. **23** (6), 881, **2021**.
 35. YU H., ZHANG Q., SUN P., SONG C. Impact of droughts on winter wheat yield in different growth stages during 2001-2016 in Eastern China. *International Journal of Disaster Risk Science*. **9**, 376, **2018**.
 36. KARIMI S., RAHEMI M., ROSTAMI A.A., SEDAGHAT S. Drought effects on growth, water content and osmoprotectants in four olive cultivars with different drought tolerance. *International Journal of Fruit Science*. **18** (3), 254, **2018**.
 37. PORKER K., STRAIGHT M., HUNT J.R. Evaluation of G×E×M interactions to increase harvest index and yield of early sown wheat. *Frontiers in Plant Science*. **11**, 994, **2020**.
 38. AHMED H., KHAN A.S., KHAN S.H., KASHIF M. Genome wide allelic pattern and genetic diversity of spring wheat genotypes through SSR markers. *International Journal of Agriculture and Biology*. **19**, 1559, **2017**.
 39. QUARRIE S., PEKIC QUARRIE S., RADOSEVIC R., RANCIC D., KAMINSKA A., BARNES J., LEVERINGTON M., CEOLONI C., DODIG D. Dissecting a wheat QTL for yield present in a range of environments: from the QTL to candidate genes. *Journal of Experimental Botany*. **57** (11), 2627, **2006**.
 40. MAJEED S., SAJJAD M., KHAN S.H. Exploitation of non-additive gene actions of yield traits for hybrid breeding in spring wheat. *Journal of Agriculture and Social Sciences*. **7** (4), 131, **2011**.
 41. FELLAHI Z.E.A., HANNACHI A., BOUZERZOUR H., BOUTEKRABT A. Line×tester mating design analysis for grain yield and yield related traits in bread wheat (*Triticum aestivum* L.). *International Journal of Agronomy*. **2013**.
 42. MUNEEB M.A., NISA Z., MUNIR M., IMRAN M., INTIKHAB A., ADIL S., SAIFULLAH N.-U.-A. Line×tester analysis for yield contributing morphological traits in *Triticum aestivum* under drought conditions. *International Journal of Agronomy and Agricultural Research*. **9** (2), 57, **2016**.
 43. MEENA H., DINESH K., SRIVASTAVA T., PRASAD S.R. Stability for grain yield and its contributing traits in bread wheat (*Triticum aestivum*). *Indian Journal of Agricultural Sciences*. **84** (12), 1486, **2014**.
 44. NIZAM S., VERMA S., SINGH K., AGGARWAL R., SRIVASTAVA K.D., VERMA P.K. High reliability transformation of the wheat pathogen *Bipolaris sorokiniana* using *Agrobacterium tumefaciens*. *Journal of Microbiological Methods*. **88** (3), 386, **2012**.
 45. SIEBERT J., SÜNNEMANN M., AUGÉ H., BERGER S., CESARZ S., CIOBANU M., GUERRERO-RAMÍREZ N.R., EISENHAUER N. The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. *Scientific Reports*. **9** (1), 639, **2019**.