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RESEARCH ARTICLE

A comprehensive study of wheat genotypes for combining ability and heritability in drought tolerance

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Abstract

A major challenge in wheat cultivation is the negative impact of water scarcity on growth and yield. Therefore, it is crucial to develop wheat varieties with both high productivity and resilience to drought stress to support food production and improve global food security. The study aims to identify general and specific combining abilities and to understand the genetic mechanisms responsible for key traits by employing half-diallel analysis. In the current study, a half-diallel set comprising 10 x 10 wheat genotypes was subjected to crosses in all feasible combinations, excluding reciprocals, under drought stress conditions. Significant mean squares were observed for both General Combining Ability (GCA) and Specific Combining Ability (SCA) components among the 10 parents and 45 F1 progenies across eleven traits. Assessment of variance components (s2g and s2s), narrow-sense heritability (Hn), broad-sense heritability (Hb) and the GCA/SCA ratio allowed for the determination of the relative contributions of additive and non-additive genetic components. High narrow-sense heritability was noted for traits such as days to 75 % flowering, spike length and biological yield, indicating their predominantly additive genetic control. Conversely, the remaining eight traits exhibited low narrow-sense heritability, suggesting their inheritance is primarily governed by non-additive genetic factors, thus indicating the potential benefits of heterosis breeding. Based on GCA effects, P5 demonstrated superior general combining ability across traits, except for biological yield. P1, P3, P8 and P9 exhibited better combining ability for grain yield per plant. Specific cross combinations including P7 × P10, P3 × P4 and P5 × P6 displayed notable specific combining ability and could be leveraged to develop superior pure lines in subsequent breeding endeavors.

Keywords

drought stress; General Combining Ability; heritability; Specific Combining Ability; wheat

Introduction

Wheat (*Triticum aestivum* L.) is a key component of global food security, providing approximately 20 % of human calorie intake and protein (1). However, shifts in global temperature and precipitation patterns are impacting crop production worldwide, including wheat. Many developing nations, including certain regions in India are experiencing more frequent drought due to these climatic changes and posing a significant threat to food supply (2, 3). Research indicates that a one–degree Celsius rise in temperature during the last 29 years contributed to a 6 % decrease in wheat production compared to expected yields unaffected by global warming. By 2025, further temperature increases, coupled with altered precipitation patterns could reduce global wheat production by 23.2–27.2 % (4, 5). Developing adaptable, high-yielding crop varieties capable of thriving in suboptimal growing conditions is imperative for sustainable agricultural growth and food security. Hybrid wheat cultivation presents an effective strategy to enhance produce and steadiness through assorted settings, thereby bolstering global wheat productivity (6, 7). Despite its potential, hybrid wheat currently occupies only 1 % of global wheat cultivation, with significant production primarily in Europe, China and India. Consequently, improving wheat cultivars to withstand drought stress conditions is paramount in wheat breeding efforts (4, 8). Successful hybrid breeding programs necessitate the efficient exploitation of heterosis, cost-effective hybridization techniques, and achieving high grain yield (9). Authors first familiarised the notion of GCA and SCA. GCA, determined by comparing the standard efficiency of all hybrids involving a particular inbred line, guides phenotypic selection based on parental breeding values. SCA, on the other hand, quantifies the deviation of hybrid performance from what is predicted by parental GCA, aiding in the identification of specific cross combinations for heterosis breeding. Diallel analysis, a common approach, is employed to gather genetic information from hybrids and parent lines, facilitating the classification of genotypes based on heterotic patterns and identification of parents with high GCA and hybrids with high SCA (11-13). The current exploration sought to evaluate the genetic attributes related to water deficit tolerance for the selection of genotypes suitable for incorporation into breeding programs aimed at developing stress-tolerant varieties through heritability and combining ability analysis. The study objectives include determining, evaluating, and estimating the patterns and expressions of GCA, SCA and heritability.

Materials and Methods

Field Experiments

The research was carried out in the Agriculture Research Field at Lovely Professional University, Phagwara (Punjab), during the Rabi seasons of 2017–18 and 2018–19. Located in Punjab, Lovely Professional University is 234 m above sea level and is between latitudes 31.2551° N and longitude 75.7050° E. In the Rabi season of 2017–18, 10 diverse wheat genotypes (IC212140, IC532889, IC82322, IC78751, IC138866, IC78737, IC55681, IC78801, IC75310, IC78837) indicated as P1, P2, P3, P4, P5, P6, P7, P8, P9 and P10 respectively were chosen and sown in 2 rows, with each row spanning 5 m in length and spaced at 25cm x 10 cm. To maintain optimal plant population density, seeds were sown singularly per hill. A half-diallel design was utilized to create 45 crosses among the 10 selected genotypes (14, 15). Forty-five hybrids' grains were developed by hand emasculation and pollination (Fig. 1). Irrigation was applied twice a season (on the 60th and 90th day) to the assessed genotypes of durum wheat and their F1 hybrids.

During the Rabi season of 2018-19, under drought stress conditions, the 45 F1 hybrids and their parental lines were cultivated using a Compact Family Randomized Block Design with 3 replications. Observations were made on various quantitative traits including days to 75 % flowering, days to maturity, plant height (cm), number of spikelets per spike, number of grains per spike, 1000-seed weight, grain yield per plant, spike length, number of tillers per plant, harvest index and biological yield (16, 17).

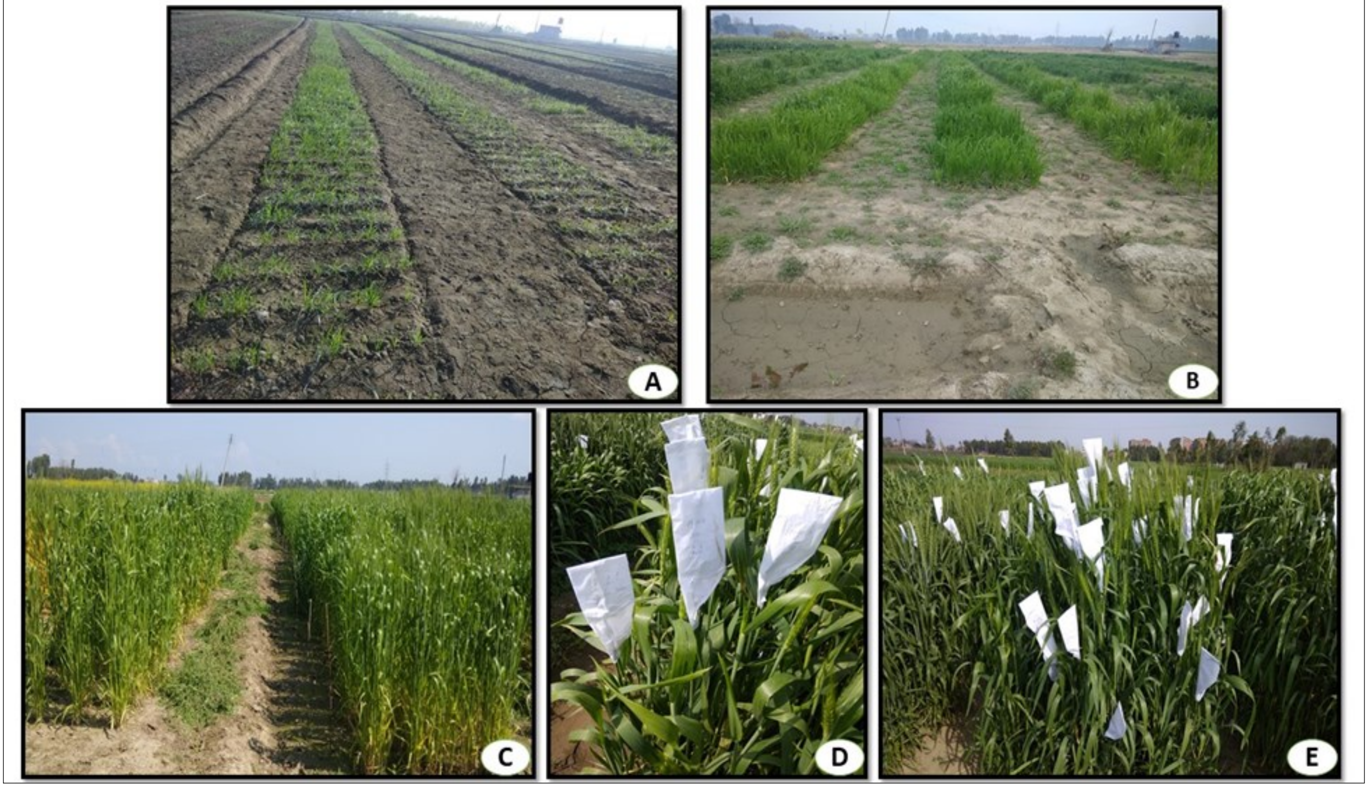

Fig. 1. (**A**) Early seedling stage, (**B**) juvenile stages, (**C**) Mature plants, (**D & E**) Bagging of spikes after emasculation and hand pollination process Bagged plants.

Statistical Analysis

The fixed model and Windostat version 9.2 from Indostat services, Hyderabad were utilized to calculate GCA and SCA using the methodologies outlined (10, 14) models 1 and 2 as follows:

$$Yijk = \mu + gi + gj + sij + \varepsilon ijk \qquad ....(1)$$

Where Yijk was the observed value of the hybrid between parents *i* and *j*. μ indicates the population means, *gi* and *gj* denote the GCA effect of *i* and *j* parents, *sij* indicates the SCA effect of *i* and *j* cross and the distinct environmental effect of jkl observation is denoted by *eijk*.

Results and discussion

The significance of the mean squares of the GCAs was highly notable ($P \leq 0.001$) for all attributes investigated as indicated by the analysis of variance (Table 1). For all attributes examined, the mean squares for SCA were also highly significant ($P \leq 0.05$ and $P \leq 0.001$). It is critical to focus on breeding pure lines and developing superior pure lines from hybrids with a high SCA effect and mean. A non-additive genetic component was responsible for controlling all attributes. Similar conclusions were also reported by earlier findings (1, 11, 18-20). For all traits, H1 component values were higher than D component values, implying a higher, non-additive gene involvement in the distribution of attributes (Table 2). The net dominance factor (h2) was found noteworthy for the days to 75 % flowering trait, while it was not significant for the other attributes. The covariance of the additive and non-additive components (F) is used in the parent population to determine the virtual frequencies of recessive and dominant alleles. The F component was not significant for any of the traits, indicating that they all contain equal amounts of dominant and recessive genes. The attributes with the highest narrow-sense heritability estimates were days to 75 % flowering, ear length and biological yield. P3, P8 and P9 were found to be strong general combiners for most attributes, while P5 was the best general cultivar for all attributes except biological yield. The parents namely K9423, GW373, PBW343, K8962, Sonalika and HD2733 were found to be the best overall combiners for grain yield and its components (5).

Based on the GCA of the parents (Table 3), genotypes P5, P7, P8, P9 and P10 were evaluated as the best general combiners for days to 75 % flowering. Four crosses, P5×P6, P7×P9, P7×P10, and P9 × P10, showed significant negative effects on specific combining ability (Supplementary Table 1) and were considered better cross combinations for early flowering. Similar results were observed for days to heading and maturity (11, 18, 21). Based on GCA effects, parents P2, P5 and P7 were considered favorable for plant height (22, 23). P1 × P3, P2 × P5 and

Table 1. Estimates of genetic variances and heritability in F1 generation Punjab.

Source of variation	DF	DTF (n)	DTM (n)	PH (cm)	NSS (n)	NGPS (n)	1000 SW (g)	GYP (g)	SL (cm)	NTPP (n)	HI (%)	BY (g m^{-2})
GCA	9	173.55***	1.11***	730.70***	2.53***	210.18***	112.43***	87.76***	4.24***	61.43***	83.90***	1699.87***
SCA	45	20.37***	1.47***	215.15***	2.47***	90.14***	34.02***	37.35***	0.74***	26.06***	21.62***	289.44***
Error	108	0.17	0.29	0.16	0.18	0.15	0.14	0.13	0.002	0.12	0.15	0.16
σ^2g		14.44	0.068	60.87	0.19	17.50	9.35	7.30	0.35	5.10	6.97	141.64
σ^2s		20.19	1.18	214.99	2.28	89.98	33.87	37.21	0.73	25.93	21.46	289.27
$H^2_{n.s}$		0.58	0.08	0.36	0.13	0.27	0.35	0.28	0.48	0.28	0.39	0.49
$H^2_{b.s.}$		0.99	0.81	0.99	0.93	0.99	0.99	0.99	0.99	0.99	0.99	0.99
GCA/ SCA		0.71	0.05	0.28	0.08	0.19	0.27	0.19	0.47	0.19	0.32	0.48

****p*** = 0.05; *****p*** = 0.01; ******p*** = 0.001 **DF**=degree of freedom, **DTF**= days to 75 % flowering, **DTM**=days to maturity, **PH**=plant height, **NSS**=number of spikelets /spike, **NGPP**= number of grains per spike,**1000 SW**=1000-seeds weight, **GYP**= grain yield/plant, **SL**=spike length, **NTPP**= number of tillers per plant, **HI**= harvesting index, **BY**= biological yield.

Table 2. Estimates of genotypic variance components and their ratios for 11 studied attributes.

Components	75% flowering (No)	DTM (No.)	PH (cm)	NSS (No.)	NGPS (No.)	1000 SW (g)	GYP (g)	SL (cm)	NTPP (No.)	HI (%)	BY (g m^{-2})
D	71.73*	0.18^{ns}	93.71*	1.05^{ns}	17.78^{ns}	24.87^{ns}	9.62^{ns}	1.58*	13.29^{ns}	21.68*	246.36*
H1	84.41*	5.35*	969.30^{ns}	9.89*	423.98*	169.44*	188.12*	0.83*	-1.81*	11.94*	1395.48*
H2	75.62*	4.98*	803.32^{ns}	9.17*	323.26*	117.68*	127.82*	2.65*	99.10*	78.26*	1033.46*
F	24.03^{ns}	0.16^{ns}	-41.46^{ns}	0.90^{ns}	21.24^{ns}	28.05^{ns}	26.73^{ns}	0.83^{ns}	-1.81^{ns}	11.94^{ns}	-82.57^{ns}
H^2	25.20*	0.89^{ns}	15.49^{ns}	0.54^{ns}	33.11^{ns}	7.88^{ns}	11.32^{ns}	0.53^{ns}	20.98^{ns}	0.87^{ns}	31.74^{ns}
E	0.17^{ns}	0.30*	0.17^{ns}	0.18^{ns}	0.16^{ns}	0.15^{ns}	0.14^{ns}	0.003^{ns}	0.13^{ns}	0.15^{ns}	0.18^{ns}

****p*** = 0.05; *****p*** = 0.01; ******p*** = 0.001, **ns** = non-significant, **DTF** = days to 75% flowering, **DTM** = days to maturity, **PH** = plant height, **NSS** = number of spikelets /spike, **NGPP** = number of grains per spike, **1000 SW** = 1000-seeds weight, **GYP** = grain yield/plant, **SL** = spike length, **NTPP** = number of tillers per plant, **HI** = harvesting index, **BY** = biological yield.

Table 3. Estimates of GCA effects of each parent for all studied traits in F1 generation in Punjab.

Parent	75 % flowering(n)	Days to maturity (n)	Plant height (cm)	No. of spikelets / spike(n)	No. of grains / spike(n)	1000 seeds weight (gm)	Grain yield/ plant (gm)	Spike height (cm)	No. of tillers / plant(n)	Harvesting index (%)	Biological yield (g m^{-2})
P1	4.27***	-0.106^{ns}	1.26***	-0.39**	2.70***	-1.63***	3.32***	-0.04***	-2.23***	5.35***	-6.96***
P2	4.36***	-0.106^{ns}	-19.72***	-0.36**	1.25***	3.85***	-1.97***	-0.29***	2.42***	1.08***	-9.55***
P3	2.22***	-0.133^{ns}	7.88***	-0.200^{ns}	5.42***	-1.13***	2.46***	1.53***	1.87***	-4.33***	23.53***
P4	3.30***	0.006^{ns}	9.36***	0.41***	-9.18***	-6.99***	-6.28***	-0.06***	1.62***	0.56***	-20.60***
P5	-3.69***	-0.522***	-1.34***	0.63***	4.95***	2.51***	1.18***	0.20***	2.84***	2.12***	-4.05***
P6	2.50***	-0.161^{ns}	1.17***	-0.33**	-1.93***	-1.31***	1.35***	-0.77***	-1.90***	-2.052***	10.75***
P7	-5.47***	-0.133^{ns}	-1.33***	-0.56***	-1.07***	1.08***	-0.70***	-0.20***	-3.96***	-1.95***	4.75***
P8	-4.83***	0.394**	0.76***	-0.14^{ns}	0.70***	2.33***	0.99***	-0.22***	-0.37***	0.59***	0.47***
P9	-1.66***	0.506***	0.90***	0.68***	-0.68***	-0.08^{ns}	0.30**	-0.009***	0.70***	-0.38***	1.31***
P10	-1.00***	0.256	1.04***	0.27*	-2.13***	1.37***	-0.67***	-0.10***	-0.98***	-0.99***	0.33***

*p = 0.05; **p = 0.01; ***p = 0.001; **ns** = non-significant, **DTF** = days to 75 % flowering; **DTM** = days to maturity; **PH** = plant height; **NSS** = number of spikelets / spike; **NGPP** = number of grains per spike; **1000 SW** = 1000-seeds weight; **GYP** = grain yield/plant; **SL** = spike length; **NTPP** = number of tillers per plant; **HI** = harvesting index; **BY** = biological yield; **P1** = IC212140; **P2** = IC532889; **P3** = IC82322; **P4** = IC78751; **P5** = IC138866; **P6** = IC78737; **P7** = IC55681; **P8** = IC78801; **P9** = IC75310; **P10** = IC78837.

P2 × P10 showed a negative and significant SCA impact, implying that they are good hybrids for plant height. Parents P2, P3, P4, P5 and P9 showed significantly positive general combining ability, indicating that these genotypes were identified as better general determinants for the number of reproductive tiller/plants. Crosses such as P1 × P9, P2 × P4, P3 × P4 and P3 × P5 showed a strong positive SCA effect, suggesting that these hybrids were the best cultivars for more reproductive tillers. Similar results were also found for the number of reproductive tillers/plants in wheat in previous studies (11, 18, 21, 24-27). P3 and P5 were identified as the best genotypes for ear length due to significantly favourable GCA influence. P1 × P6, P2 × P6, P3 × P9 and P4 × P10 showed a strong positive influence of specific combining ability on the trait ear length; similar observations were also made in previous findings (21, 24-27).

The parents P2, P5, P7, P8 and P10 exhibited significant and positive general combining effects, suggesting their superiority as genotypes for 1000-grain weight. Notably, cross combinations such as P1 × P3, P5 × P8, P7 × P10 and P8 × P9 demonstrated strong positive SCA impacts on the trait of 1000-grain weight, indicating their effectiveness as combiners for this trait. Similarly, cultivars P1, P2, P3, P5 and P8 displayed significant positive general combining effects, establishing them as good general combiners for the number of grains per spike. Cross combinations like P2 × P5, P2 × P6, P3 × P8, P7 × P10 and P8 × P9 showcased significant and favourable SCA effects for the number of grains per spike, further reinforcing their efficacy as combiners for this trait. These findings align with previous studies on wheat (11, 20, 21).

The best general combiners for grain yield per plant were identified as P1, P3, P5, P6, P8 and P9. Notably, crosses such as P1 × P4, P2 × P4, P3 × P4 and P6 × P10 exhibited considerable positive SCA impacts on grain yield per plant, consistent with previous findings (11, 20, 21, 24-26). Cultivars P3, P6, P7, P8, P9 and P10 were recognized as good general combiners for biological yield, with crosses like P1 × P4, P1 × P5, P1 × P6 and P1 × P10 showing positive effects for biological yield. For the harvest index, cultivars P1, P2, P4, P5 and P9 exhibited significant positive general combining effects, while only crosses such as P1 × P3, P1 × P4 and P2 × P6 demonstrated positive and significant SCA effects on the harvest index. These observations are consistent with previous studies (11, 20, 21).

Among the 11 parameters studied, additive genetic variance (D) components were found to be significant for Days to 75 % flowering, plant height, spike length, harvest index and biological yield per plant. A study reported significant additive variance factors for spike height, plant height and 1000-kernel weight (28). Additionally, both H1 and H2 components were significant for all traits except plant height. The predominance of the H1 component over the D component suggests a substantial role of non-additive gene expression in trait transmission to subsequent generations. Furthermore, traits with low GCA/SCA ratios indicate the influence of non-additive genetic factors. Similarly found that all studied traits were under non-additive gene effects (5), supported by a low GCA/SCA ratio of less than one, although the h2 component was only significant for days to 75 % flowering. These findings are consistent with earlier observations (28). As a result, potential segregants may be expected from these hybrids and may be applied to improve these traits in both ideal and drought-stressed conditions (29).

Conclusion

Genotypes P1, P3, P5, P6, P8 and P9 were acknowledged as the top overall combiners for grain yield per plant after an overall evaluation of the effects of GCA in the current trial under water-deficient conditions. Crosses P1 × P4, P2 × P4, P3 × P4 and P6 × P10 demonstrated the strong positive effect of SCA on grain yield per plant. There are both additive and non-additive variations, suggesting that these parents and crosses are suitable for subsequent breeding initiatives. Therefore, to take advantage of both additive and non-additive factors for the genetic improvement of wheat under moisture stress, it is advisable to use semi-dial crosses with frequent selection and parentage screening.

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Authors' contributions

SK performed experimental work and writing of research article. AK - Idea development, proofreading, advising, and guidance throughout the work.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None.

Supplementary data

Supplementary Table 1. Estimation of specific combining ability (SCA) effects for 11 characteristics in F1 generation in Punjab.

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