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# PHYSICAL AND MORPHOLOGICAL MARKERS FOR ADAPTATION OF DROUGHT-TOLERANT WHEAT TO ARID ENVIRONMENTS

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The threat of climate change has instilled a demand for multi-faceted genetic diversity coupled with resourceful tools and technologies to attain biotic and abiotic resistance in crops. The present study was designed to investigate and compare common physiological and morphological traits under normal and water-stressed conditions. Seven selected (Pakistani, Indian and CIMMYT) water stress-tolerant (WST) genotypes were crossed with seven local water stress-susceptible (WSS) lines using a line × tester mating approach. The hybrids, together with parents, were sown in two different environments. Combining ability effects determined the behavior of both parents as well as offspring and allowed the best combiners for different traits to be selected. Different traits showed additive and non-additive types of gene action under both environmental conditions. The present study concluded that genotypes Nesser, Dharwar Dry, Inqilab-91, among others, served as good combiners while Bakhar-2002 × 9247, Dharwar Dry × 9021, Bakhar-2002 × 9244, and Nesser × 9244 are promising cross combinations. Regarding grain yield, genotype 9252 and Dharwar Dry performed best under normal irrigation and water-stressed conditions, respectively. A change in water provision resulted in a shift in gene action, broad sense heritability and proportional share that each trait contributed. When these traits were pooled, it was possible to discriminate between WST and WSS genotypes and, through line × tester experiments, develop drought- and water stress-tolerant lines based on morphological markers under changing climatic conditions.
**Keywords:** Breeding, climate, food security, line × tester, water stress

## INTRODUCTION

Agriculture is a complex sector and mainly depends upon climate, soil and its health, water availability, heat and rainfall, which are the prime drivers of growth in agriculture. It is a matter of grave concern for agriculturists and plant scientists that the global mean temperature is expected to rise, thereby reducing crop production while yield in Asian and Mediterranean regions will be considerably more vulnerable (Martiniello and Teixeira da Silva, 2011; Hossain and Teixeira da Silva 2013a,b; Noorka and Heslop-Harrison 2014). The Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report revealed that rises in mean global temperatures will be as high as 2-4°C by 2100 (IPCC 2007). This rise in temperature will lead to further global warming (IPCC, 2007) and approximately 20% loss in soil moisture (Scheiermeier, 2008). Data from the last 60 years depicted that seasonal temperature throughout the world is increasing each year (NASA 2011). The continuous and combined effect of temperature and water stress menaces the stability of crop production (Hossain *et al.,* 2012; Noorka, 2014).

Wheat (*Triticum aestivum* L.) is Pakistan's most important food staple and thus nourishment. Drought is the most serious environmental stress created by the interaction between climatic and meteorological factors in which inadequate water hampers the regular functioning of a crop. That is why it has been a prime breeding agenda for decades. Physiologically, water stress takes place when available moisture is reduced up to a point where plant growth is restricted (Chowdhry *et al.,* 1999; Noorka *et al.,* 2012).

According to a rough estimate, 33% of the world's arable land suffers from water stress, occasional drought, and prolonged drought, all of which reduce crop yield (Nachit and Elouafi, 2004; Noorka *et al.,* 2009) Consequently, water stress has received the greatest attention from physiologists and plant breeders involved in breeding adaptation to drought-prone environments by well-fitted adaptive features of plant growth rather than by focusing merely on a single character through functional genetic analysis (Zhu, 2001). Water is a major factor limiting plant growth, particularly wheat, resulting in stunted growth, less flowering, reduced pollination, and poor quality and grain filling (Noorka and Teixeira da Silva, 2012). Drought has affected 5.18 million ha of winter wheat in China (FAO, 2011) and 10.3 million ha in Russia, reducing output by 50 million tons (FAO, 2010). Sustainable agriculture is under threat due to many factors like water stress, particularly in Asia where irrigated agriculture is dependent upon fresh water (Wang *et al.,* 2002; Noorka, 2011). In such areas where irrigation is the only life-line for wheat crop production, the onset of drought poses a serious threat to food security (Nachit and Elouafi, 2004; Hossain *et al.,* 2012). The development of stress-tolerant varieties is a judicial way of mitigating the vagaries of abiotic stresses (Ruan and Teixeira da Silva, 2011) and the best way to tackle them is by developing stress-tolerant varieties for optimum conditions (Prasad *et al.,* 2008; Nouri *et al.,* 2011; Hossain and Teixeira da Silva, 2012).

New crosses and genetic diversity ensure the successful breeding of a wheat crop to produce a sound generation. Crop plant hybridization and analysis of combining ability provide useful information to evaluate and improve a series of traits such as water stress tolerance, physiological behavior and morphological preference to ensure long-term food security (Rajaram *et al*., 1996; Placido *et al*., 2013).

The present study was designed to determine the nature and extent of variation on different physical and morphological traits and their genetic insights to select viable wheat genotypes for successive generations to be used in further research programs to ensure food security.

## MATERIALS AND METHODS

The experiment was conducted at the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan. One hundred wheat varieties/lines, both local and exotic, were screened for water stress and all genotypes were test-selected (Noorka and Khaliq, 2007). Considering the emergence percentage, emergence rate index, mean emergence time, energy of emergence, and survival after desiccation, a cluster of 14 diverse genotypes was selected. Seven genotypes showed water stress-tolerant behavior and were selected and used as lines (female parents), namely Nesser (The International Maize and Wheat Improvement Center, known by its Spanish acronym, CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO, or CIMMYT), Dharwar Dry (India), GA-2002, Bakhar-2002, Chakwal-86, Inqilab-91 and Kohistan-97 while seven water stress-susceptible genotypes were selected as testers (male parents), namely, 9244, 9247, 9258, 9267, 9316, 9021 and 9252 (University of Agriculture lines) (Noorka and Khaliq, 2007). These genotypes and lines were used in crosses using the "line × tester mating design" described by Kempthorne (1957) in a randomized complete block design (RCBD) with three replications. All $F_1$s and their parents were sown in lines 30-cm apart keeping a plant-to-plant distance of 15 cm (GOP, 2007; Khan *et al.,* 2007; Wu *et al.,* 2010) in two irrigation conditions. The first was normal irrigation in which plants were irrigated at three vulnerable growth stages: crown root stage or tillering (35 days after sowing; DAS), booting stage (85 DAS) and milk ripe stage (112 DAS) (Khan, 2003). The total amount of water applied was calculated (Chaudhary, 2003). In the second condition, only a single surface irrigation was applied at 35 DAS to introduce water stress. Two seeds were planted per hole and only robust seedlings were used after germination. Each treatment was represented by a single line 5 m long containing 33 plants.

At 115 DAS, when the crop was fully developed, physiological and morphological traits were measured, namely stomatal frequency and size, epidermal cell size, leaf venation, flag leaf area, plant height and grain yield per plant.

***Physiological studies*:** Leaf strips of about 5 cm in length were removed from the middle portion of five fresh flag leaves of 115–DAS plants at random from each treatment in the morning when the leaves were fully turgid. These strips were immediately dipped in Conroy's solution for about 48 h to remove chlorophyll from the tissues and to arrest stomatal movement (Conroy *et al.,* 1988). The solution consisted of absolute alcohol, glacial acetic acid and pure chloroform (100: 16: 50, v/v). After 4-5 days, the strips were washed with acetone and stored in absolute alcohol for further examination. Leaf strips were observed under low (10X) magnification to count the number of stomata per microscopic field. Five observations were made for each strip and then the average was calculated. Stomatal size was measured in μm with the help of an ocular micrometer (scale = 10 mm) which was standardized using a 1.0 mm stage micrometer. Epidermal cell size (length and width) was also measured with the ocular micrometer at 40X magnification.

***Statistical analyses*:** Data recorded from both sets of experiments (normal irrigation and water stress) was pooled and analyzed using analysis of variance (ANOVA) as described by Steel *et al.* (1997). Significant differences between means were further assessed using the least significant difference (LSD) at $P < 0.01$ and $P < 0.05$. Thereafter, estimates of combining ability were computed by using the line × tester analysis method, i.e., general combining ability (GCA) and specific combining ability (SCA) (Kempthorne, 1957).

## RESULTS

In the present study, sufficient variability was observed by 7 physio-morphological traits under both normal irrigation and water stress conditions. Differences among genotypes were highly significant for most traits, indicating high variability among genotypes with significant differences in the treatments and environment × genotype interactions for all 7 traits (Table 1). By further partitioning these genotypes into parental genotypes, namely lines and testers, their crosses and environment interactions were also observed to be significant for both irrigation stress and control conditions (Table 2). Genetic variability, combining ability and type of gene action were estimated to determine the value of a source population.

**Table 1. Mean squares values from a pooled analysis of variance of 63 wheat genotypes under normal irrigation and water stress conditions**

| SOV | df | PH | FLA | SF | SS | ECS | LV | GY |
|---|---|---|---|---|---|---|---|---|
| Replication | 2 | 0.45 | 91.24 | 3537069 | 2.66 | 0.81 | 1296.19 | 6.02 |
| Treatments | 1 | 72.92** | 36021.43** | 181359702* | 16971.37** | 4835.02** | 545323.00** | 4294.13** |
| Error (1) | 2 | 54.44 | 1.96 | 17 | 4655.30 | 2778636.10 | 0.46 | 6.42 |
| Genotypes | 62 | 1.36** | 216.79** | 2279870** | 271.03** | 37.51** | 22635.66** | 60.56** |
| T×G | 62 | 41.72** | 10.78** | 46** | 3972.11* | 176481.76 | 1.18** | 5.61* |
| Error (2) | 248 | 20.28 | 5.48 | 16 | 2877.53 | 115157.09 | 0.38 | 3.75 |
| Total | 377 | | | | | | | |

*,** significant at the 5% and 1% probability level, respectively (LSD test)
SOV = source of variation, df = degree of freedom, PH = plant height (cm), FLA = flag leaf area ($cm^2$), SF = stomatal frequency, SS = stomatal size ($\mu m^2$), ECS = epidermal cell size ($\mu m^2$), LV = leaf venation, GY = grain yield (g), T×G = treatment and genotype interaction.

**Table 2. Mean squares values from analysis of variances of 7 lines and 7 testers in wheat under normal irrigation and water stress**

| SOV | df | PH | | FLA | | SF | | SS | | ECS | | LV | | GY | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | N | S | N | S | N | S | N | S | N | S | N | S | N | S |
| Rep | 2 | 0.2 | 0.6 | 140.2** | 5.4 | 0.4 | 2.3 | 5.3 | 14.3 | 4182 | 1768 | 6.0d+5** | 3.2e+5* | 8.5 | 3.92 |
| Gen | 62 | 0.6** | 1.8** | 90.0** | 168.4** | 33.3** | 14.9** | 136.5** | 180.8-** | 14949** | 11658** | 1.5e+4** | 9.0e+5** | 37.1** | 29.06** |
| Par | 13 | 259.4** | 299.3** | 44.5** | 44.3** | 239.9** | 465.8** | 25741.1** | 26048.9** | 58e+4** | 35e+5** | 0.5 | 4.3** | 46.0** | 52.13** |
| P v C | 1 | 27.3 | 53.7 | 28.7 | 16.1* | 81.7* | 285.1** | 7493.5 | 14592.1* | 10e+6** | 59e+5** | 0.0 | 0.01 | 8.4 | 25.99** |
| Cross | 48 | 45.4** | 135.4** | 30.4** | 6.9** | 109.7** | 101.4** | 12182.3** | 7699.4** | 220823 | 94782 | 0.7** | 1.2** | 35.2** | 22.88** |
| Line | 6 | 198.6** | 517.1** | 107.7** | 44.6** | 400.9** | 372.7** | 41960.3** | 5977.4** | 143484 | 97466 | 0.5 | 7.8** | 96.8** | 72.82** |
| Test | 6 | 1.1 | 0.4 | 128.4** | 345.1** | 49.5** | 2.9 | 451.6** | 394.5** | 50792** | 50868** | 1.1e+5** | 3.8e+5** | 101.6** | 49.60** |
| L x T | 36 | 6.1 | 36.8** | 14.3* | 1.2 | 4.2 | 7.4 | 784.3 | 791.5 | 87220 | 46987 | 0.6** | 0.27 | 13.9** | 10.09** |
| Error | 124 | 25.5 | 14.9 | 8.5 | 2.4 | 16.2 | 15.9 | 3609.4 | 2145.6 | 155474 | 74839 | 0.3 | 0.38 | 5.7 | 1.80 |

*,** significant at the 5% and 1% probability level, respectively
SOV = source of variation, df = degree of freedom, N = normal, S = water stressed, PH = plant height (cm), FLA = flag leaf area ($cm^2$), SF = stomatal frequency, SS = stomatal size ($\mu m^2$), ECS = epidermal cell size ($\mu m^2$), LV = leaf venation, GY = grain yield (g), Rep = replication, Gen = genotype, Par = parent, PvC= parent versus cross, L×T = line and tester interaction.

***GCA effects among lines (female parents) and testers (male parents) under normal irrigation and water stress***: The priority trait(s) are usually defined by the "clients", "end-users" or "stakeholders" and the best breeding programs, as measured by their success, are those fitting genotypes into a target agro-ecosystem; i.e. following a so-called demand-driven, system approach for developing genetically enhanced, seed-embedded technology. Considerable variation was found among the 7 lines and testers with regards to GCA effects for various traits

**Table 3. Estimates of general combining ability effects of 7 lines (female parents) and 7 testers (male parents) in wheat under normal irrigation and water stress**

| Lines/tester | PH | | FLA | | SF | | SS | | ECS | | LV | | GY | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | S | N | S | N | S | N | S | N | S | N | S | N | S |
| Nesser | -5.56 | -1.31 | -1.38 | -0.55 | -7.65 | -4.30 | -85.08 | -28.52 | 45.15 | 106.73 | -0.01 | -0.80 | 3.18 | 1.96 |
| Dharwar Dry | 4.63 | 8.93 | 3.56 | 1.59 | 2.47 | 5.00 | 52.82 | -2.12 | 77.17 | -14.78 | 0.27 | 0.75 | 2.77 | 3.16 |
| GA-2002 | 0.11 | -0.83 | -1.95 | -1.60 | -2.88 | -5.05 | 8.98 | -3.18 | 98.85 | 6.99 | -0.20 | -0.53 | -0.27 | -1.59 |
| Bakhar-2002 | -0.18 | -1.12 | -0.39 | -1.94 | 3.35 | 3.32 | -24.87 | -8.97 | -108.26 | 17.34 | 0.18 | -0.18 | -1.58 | -0.87 |
| Chakwal-86 | -0.41 | -0.07 | -2.14 | 0.22 | 2.83 | 3.39 | 29.43 | 23.94 | -78.76 | -124.10 | -0.06 | -0.16 | -2.05 | -1.39 |
| Inqilab-91 | -0.56 | -7.73 | 2.74 | 1.83 | 4.15 | 1.29 | 19.81 | 14.36 | 31.52 | -11.23 | -0.06 | 0.82 | -0.32 | 0.06 |
| Kohistan-97 | 1.97 | 2.12 | -0.44 | 0.45 | -2.27 | -3.65 | -1.09 | 4.49 | -65.68 | 19.04 | -0.11 | 0.11 | -1.73 | -1.33 |
| 9244 | -0.65 | 0.36 | 1.54 | 0.27 | -2.57 | -3.54 | -26.11 | -48.76 | -42.72 | 197.28 | 0.13 | 0.09 | -0.48 | -0.25 |
| 9247 | -3.51 | -4.12 | -1.38 | -0.34 | -4.18 | -6.14 | 57.34 | 87.87 | 199.44 | 96.99 | -0.11 | -0.05 | -1.10 | -1.39 |
| 9258 | -0.94 | -5.50 | -1.46 | 0.23 | 3.33 | -2.51 | 65.33 | 45.16 | 290.03 | 56.31 | -0.16 | 0.10 | -1.83 | -0.43 |
| 9267 | -0.80 | 0.65 | -1.56 | 0.03 | -3.56 | 0.48 | 27.61 | -2.37 | -78.04 | -51.32 | -0.11 | 0.13 | -1.26 | -1.63 |
| 9316 | 3.01 | 6.41 | 2.14 | -0.19 | -4.25 | 1.48 | -55.76 | -17.47 | -234.46 | 25.06 | 0.18 | -0.25 | 2.67 | 1.63 |
| 9021 | -0.70 | -0.83 | -0.10 | -0.54 | 5.47 | 5.93 | -39.81 | -29.93 | 176.22 | -183.27 | -0.30 | -0.10 | -1.60 | -0.47 |
| 9252 | 3.58 | 3.03 | 0.82 | 0.53 | 5.76 | 4.31 | -28.59 | -34.49 | -310.47 | -141.06 | 0.37 | 0.08 | 3.60 | 2.54 |
| SE(GCA) lines | 1.10 | 0.84 | 0.64 | 0.34 | 0.88 | 0.87 | 13.11 | 10.11 | 86.04 | 59.70 | 0.13 | 0.14 | 0.52 | 0.29 |
| SE(GCA)tester | 1.10 | 0.84 | 0.64 | 0.34 | 0.88 | 0.87 | 13.11 | 10.11 | 86.04 | 59.70 | 0.13 | 0.13 | 0.52 | 0.29 |

N = normal, S = water stressed, PH = plant height (cm), FLA = flag leaf area ($cm^2$), SF = stomatal frequency, SS = stomatal size ($\mu m^2$), ECS = epidermal cell size ($\mu m^2$), LV = leaf venation, GY = grain yield (g); SE (GCA) lines = standard error for general combining ability for lines, SE (GCA) tester = standard error for general combining ability for tester

(Table 3). In this breeding program, yield is the prime objective, so, among lines and testers, significant performance (maximum positive values) was observed for the following genotypes with respect to specific traits under stressed or control conditions: flag leaf area (Dharwar Dry and 9316 under normal irrigation; Inqilab-91 and 9252 under water stress); stomatal frequency (Inqilab-91 and 9252 under normal irrigation; Dharwar Dry and 9021 under water stress), leaf venation (Dharwar Dry and 9252 under normal irrigation; Dharwar Dry and 9267 under water stress) and grain yield (Nesser and 9252 under normal irrigation; Dharwar Dry and 9252 under water stress). Similarly, maximum negative values of GCA effects were observed for specific genotypes and traits: plant height (Nesser and 9247 under normal irrigation; Inqilab-91 and 9258 under water stress), stomatal size (Nesser and 9316 under normal irrigation; Nesser and 9244 under water stress); epidermal cell size (Bakhar-2002 and 9252 under normal irrigation; Chakwal-86 and 9021 under water stress). In each of these cases, the genotypes listed under the specified conditions were considered to be the best general combiners.

**Table 4. Estimates of specific combining ability effects of 49 wheat crosses obtained from 7 lines (female parents) and 7 testers (male parents) under normal irrigation and water stress**

| Crosses | PH | | FLA | | SF | | SS | | ECS | | LV | | GY | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | S | N | S | N | S | N | S | N | S | N | S | N | S |
| Nesser x 9244 | -0.01 | 0.16 | 0.39 | 1.63 | 1.42 | -0.82 | 6.30 | 3.25 | -272.90 | 33.29 | 0.73 | -0.13 | 3.39 | 2.10 |
| Nesser x 9247 | 0.18 | 3.31 | -1.44 | - 1.05 | -0.06 | 0.74 | 23.60 | -32.01 | -244.20 | 86.61 | - 0.37 | -0.02 | -1.97 | -2.96 |
| Nesser x 9258 | 0.60 | -0.31 | -0.20 | - 0.25 | 1.76 | 0.21 | -15.92 | -17.42 | -127.80 | -30.91 | - 0.32 | 0.005 | 0.24 | 0.85 |
| Nesser x 9267 | -0.20 | -4.12 | -1.13 | - 0.21 | -0.86 | 1.49 | -10.82 | 3.83 | 146.52 | -155.6 | - 0.03 | -0.06 | -2.54 | -1.45 |
| Nesser x 9316 | -1.01 | 1.12 | 1.89 | 0.08 | -0.16 | 0.49 | -1.33 | 46.02 | 324.29 | 82.68 | 0.68 | 0.28 | 2.37 | 3.03 |
| Nesser x 9021 | -0.63 | -0.98 | -0.55 | - 0.29 | -1.52 | 1.90 | -11.40 | -7.20 | 111.64 | -43.95 | -0.18 | 0.07 | -3.43 | -3.27 |
| Nesser x 9252 | 1.08 | 0.83 | 1.05 | 0.08 | -0.57 | -4.01 | 9.58 | 3.53 | 62.50 | 27.88 | -0.51 | -0.14 | 1.94 | 1.71 |
| D. Dry x 9244 | -0.54 | -0.41 | 0.19 | - 0.42 | -0.12 | 1.21 | 3.98 | 2.07 | 195.30 | 147.78 | 0.11 | -0.18 | - 4.04 | -2.36 |
| D. Dry x 9247 | -0.68 | 3.07 | 0.59 | 1.04 | -0.51 | 2.14 | -18.89 | -8.60 | 62.69 | -94.38 | -0.32 | -0.37 | -2.45 | -0.36 |
| D. Dry x 9258 | 0.08 | 4.45 | -0.93 | 0.44 | -0.76 | 1.51 | -8.05 | 12.45 | 33.04 | 25.18 | -0.27 | -0.45 | -1.79 | -3.82 |
| D. Dry x 9267 | -0.73 | 2.97 | 1.39 | -0.32 | 0.86 | -0.81 | -2.50 | -11.32 | -162.20 | 51.56 | 0.35 | 0.48 | 5.73 | 1.78 |
| D. Dry x 9316 | 1.13 | -2.46 | -0.36 | 0.51 | 0.62 | 0.82 | 6.68 | 0.77 | 81.34 | 30.40 | -0.60 | 0.23 | 1.41 | 1.29 |
| D. Dry x 9021 | 1.84 | -6.88 | -2.24 | -0.46 | -0.37 | - 4.67 | 15.42 | 3.91 | -159.20 | -183.0 | 0.87 | 0.25 | 0.30 | 2.06 |
| D. Dry x 9252 | -1.11 | -0.74 | 1.36 | -0.79 | 0.28 | - 0.21 | 3.37 | 0.74 | -50.94 | 22.49 | -0.13 | 0.04 | 0.84 | 1.41 |
| GA-02 x 9244 | -0.68 | -1.98 | -2.68 | 0.20 | -0.04 | 0.59 | 7.75 | 9.52 | 26.18 | -12.71 | -0.41 | -0.07 | 1.13 | 0.32 |
| GA-02 x 9247 | -0.16 | -3.50 | 0.71 | 0.57 | -1.82 | - 0.81 | -11.70 | -16.45 | 117.81 | -186.1 | 0.49 | 0.41 | 1.72 | 1.39 |
| GA-02 x 9258 | -2.39 | -2.79 | -2.29 | 0.25 | 0.03 | 1.23 | 3.88 | -4.00 | 58.59 | 18.55 | 0.20 | 0.03 | 0.23 | -0.50 |
| GA-02 x 9267 | -0.87 | 2.07 | 1.68 | 0.36 | -0.35 | 0.57 | -0.58 | 7.29 | 183.87 | 4.93 | -0.18 | -0.04 | -0.79 | 1.33 |
| GA-02 x 9316 | 0.65 | 4.64 | 2.24 | -1.57 | -1.19 | 0.24 | 6.35 | -8.79 | -370.70 | -18.25 | -0.13 | -0.56 | - 3.25 | -2.16 |
| GA-02 x 9021 | 2.03 | 1.21 | 1.40 | -0.12 | 0.88 | -0.22 | -4.04 | 2.13 | -7.50 | 213.03 | -0.65 | 0.13 | -0.13 | 0.17 |
| GA-02 x 9252 | 1.41 | 0.35 | -1.05 | 0.31 | 2.50 | -1.59 | -1.66 | 10.31 | -8.26 | -19.48 | 0.68 | 0.08 | 1.08 | -0.54 |
| Bak-02 x 9244 | 2.60 | 8.31 | 5.27 | 0.01 | 0.19 | -0.28 | -17.89 | -1.84 | 129.63 | 116.68 | -0.46 | -0.12 | 0.11 | 0.66 |
| Bak-02 x 9247 | -2.54 | -4.88 | -1.99 | -0.73 | 1.57 | -0.45 | 30.30 | 18.30 | -83.35 | 54.25 | 0.11 | -0.07 | 1.17 | 0.40 |
| Bak-02 x 9258 | -0.44 | -3.17 | -1.42 | -0.17 | -0.44 | -1.14 | 25.60 | -14.53 | 194.76 | -76.02 | 0.49 | 0.31 | 0.23 | 4.07 |
| Bak-02 x 9267 | -0.58 | 1.35 | -0.01 | 0.53 | 0.31 | -0.47 | 32.98 | 11.06 | -279.60 | 63.19 | -0.56 | 0.34 | -1.34 | -0.69 |
| Bak-02 x 9316 | 1.94 | 1.92 | -0.58 | 0.44 | 0.003 | -1.50 | -26.64 | -17.92 | 77.48 | -131 | 0.16 | -0.04 | -0.53 | -2.44 |
| Bak-02 x 9021 | -0.35 | 0.16 | -0.81 | -0.08 | -1.29 | 1.48 | -32.92 | 11.51 | 126.89 | 65.41 | -0.03 | -0.09 | -0.10 | -0.61 |
| Bak-02 x 9252 | -0.63 | -3.69 | -0.47 | 0.001 | -0.34 | 2.37 | -11.44 | -6.59 | -165.80 | -92.0 | 0.30 | -0.33 | 0.46 | -1.40 |
| Chak-86 x 9244 | -2.49 | -3.07 | 0.08 | 0.01 | -0.82 | -0.18 | -2.34 | -7.60 | 12.98 | -139.6 | -0.22 | 0.42 | - 0.37 | -0.21 |
| Chak-86 x 9247 | 2.03 | 2.73 | -0.11 | 0.24 | 0.36 | -0.52 | -12.48 | 2.41 | -29.27 | -173.9 | 0.68 | -0.13 | 1.67 | 0.74 |
| Chak-86 x 9258 | 0.13 | -0.22 | 0.32 | - 0.12 | -1.39 | -0.88 | 9.89 | 5.84 | 154.11 | -5.6 | 0.06 | 0.02 | 0.47 | 0.83 |
| Chak-86 x 9267 | 1.32 | -0.69 | 0.85 | - 0.14 | 0.60 | -0.53 | -19.32 | 17.07 | 80.49 | 140.7 | 0.01 | -0.15 | 0.93 | -0.50 |
| Chak-86 x 9316 | -2.16 | -2.79 | -1.81 | 0.58 | 0.13 | 0.47 | 7.04 | -9.54 | -209.50 | 161.2 | -0.27 | -0.10 | -2.20 | 0.37 |
| Chak-86 x 9021 | -0.11 | 1.45 | 1.83 | - 0.09 | 1.57 | 0.34 | 11.67 | -6.20 | -110.10 | -102.5 | -0.13 | -0.05 | 1.16 | 0.58 |
| Chak-86 x 9252 | 1.27 | 2.59 | -1.16 | - 0.47 | -0.45 | 1.30 | 5.53 | -1.97 | 101.32 | 119.8 | -0.13 | -0.02 | -1.67 | -1.81 |
| Inqilab-91 x 9244 | 0.32 | -4.74 | -0.84 | - 0.43 | -0.01 | -0.08 | -6.37 | -4.50 | -35.48 | -136.4 | -0.22 | -0.45 | 0.64 | 0.40 |
| Inqilab-91 x 9247 | 1.51 | 1.73 | -0.33 | 0.08 | 1.57 | -1.21 | -6.11 | 0.09 | 48.20 | 165.1 | -0.32 | -0.11 | 0.91 | 1.07 |
| Inqilab-91 x 9258 | 0.94 | 1.12 | 3.48 | -0.69 | -0.91 | -0.77 | 3.94 | 10.56 | -206.7 | 24.6 | -0.60 | -0.08 | -0.73 | -1.66 |
| Inqilab-91 x 9267 | 0.13 | -1.36 | -5.59 | 0.06 | 0.51 | 1.24 | 4.66 | 11.09 | 120.6 | -99.7 | 0.35 | -0.22 | -1.37 | -1.06 |
| Inqilab-91 x 9316 | -0.35 | 1.88 | 1.89 | -0.37 | 1.20 | -0.03 | -10.49 | -9.76 | 172.3 | 91.34 | 0.73 | 0.42 | 2.59 | 0.95 |
| Inqilab-91 x 9021 | -1.97 | -1.22 | -0.43 | 0.36 | -1.22 | 1.11 | 19.39 | -4.40 | -112.4 | -110.5 | -0.13 | 0.11 | -1.04 | -0.28 |
| Inqilab-91 x 9252 | -0.58 | 2.59 | 1.81 | 0.98 | -1.14 | -0.26 | -5.02 | -3.07 | 13.48 | 65.65 | 0.20 | 0.33 | -1.01 | 0.57 |
| Koh-97 x 9244 | 0.80 | 1.73 | -2.41 | - 0.99 | -0.62 | -0.44 | 8.58 | -0.89 | -55.69 | -9.02 | 0.49 | 0.52 | -0.87 | -0.91 |
| Koh-97 x 9247 | -0.35 | -2.46 | 2.57 | -0.15 | -1.10 | 0.12 | -4.72 | 36.26 | 128.1 | 148.4 | -0.27 | 0.29 | -1.05 | -0.30 |
| Koh-97 x 9258 | 1.08 | 0.92 | 1.05 | 0.53 | 1.72 | -0.17 | -19.34 | 7.10 | -105.9 | 44.27 | 0.44 | 0.15 | 1.35 | 0.24 |
| Koh-97 x 9267 | 0.94 | -0.22 | 2.80 | -0.28 | -1.06 | -1.49 | -4.42 | -39.01 | -89.72 | -5.07 | 0.06 | -0.35 | -0.63 | 0.60 |
| Koh-97 x 9316 | -0.20 | -4.31 | -3.27 | 0.33 | -0.60 | -0.49 | 18.39 | -0.77 | -75.23 | -215.8 | -0.56 | -0.24 | -0.39 | -1.05 |
| Koh-97 x 9021 | -0.82 | 6.26 | 0.80 | 0.67 | 1.94 | 0.05 | 1.88 | 0.25 | 150.73 | 161.5 | 0.25 | -0.42 | 3.24 | 1.35 |
| Koh-97 x 9252 | -1.44 | -1.93 | -1.54 | -0.12 | -0.28 | 2.41 | -0.38 | -2.93 | 47.75 | -124.3 | -0.41 | 0.04 | -1.65 | 0.06 |
| SE (SCA) effect | 2.92 | 2.23 | 1.69 | 0.89 | 2.32 | 2.31 | 34.67 | 26.70 | 227.6 | 157.9 | 0.36 | 0.36 | 1.38 | 0.77 |

N = normal, S = water stressed, PH = plant height (cm), FLA = flag leaf area ($cm^2$), SF = stomatal frequency, SS = stomatal size ($\mu m^2$), ECS = epidermal cell size ($\mu m^2$), LV = leaf venation, GY = grain yield (g) SE (SCA) = standard error for specific combining ability.

***SCA effects of wheat crosses under normal irrigation and water stress*:** The SCA effects for 49 cross combinations resulting from the crosses between 7 lines (L) and 7 testers (T) under normal irrigation and water stress are presented in Table 4 and summarized as values representing L × T SCA in cross combinations for the following traits. Plant height: Bakhar-2002 × 9247 (normal irrigation) = -2.54; Dharwar Dry × 9021 (water stress) = -6.88. Similarly, for flag leaf area: Bakhar-2002 × 9244 (normal irrigation) = 5.27; Nesser × 9244 (water stress) = 1.63. Stomatal frequency: GA-2002 × 9252 (normal irrigation) = 2.50; Kohsitan-97 × 9252 (water stress) = 2.41. Stomatal size: Bakhar 2002 × 9021 (normal irrigation) = -32.92; Kohistan-97 × 9267 (water stress) = -39.01. Epidermal cell size: GA-2002 × 9316 (normal irrigation) = -370.69; Kohistan-97 × 9316 (water stress) = -215.87. Leaf venation: Dharwar Dry × 9021 (normal irrigation) = 0.87; Kohistan-97 × 9244 (water stress) = 0.52. Grain yield: Dharwar Dry × 9267 (normal irrigation) = 5.73); Bakhar-2002 × 9258 (water stress) = 4.07. All genotypes listed were the best combiners for the indicated traits. Higher GCA effects denote an additive type of gene action under normal irrigation while, under water stress, the SCA effect assumed greater importance.

***Estimates of genetic variance under normal irrigation and water stress*:** Table 5 reveals the differences between variances due to GCA ($\sigma^2$gca), SCA ($\sigma^2$sca), the ratio between GCA and SCA ($\sigma^2$sca/$\sigma$2sca) and the degree of dominance between dominance variance ($\sigma^2$D) and additive variation ($\sigma^2$A), estimates of phenotypic variance ($\sigma^2$p), genotypic variance ($\sigma^2$g) and broad-sense heritability. Under normal irrigation, the estimates depicted higher GCA genetic effects for stomatal frequency, stomata size, epidermal cell size and plant height. Under water stress, the genetic mode had shifted.

***Proportional contribution of lines, testers and their interactions under normal irrigation and water stress*:** Observing the contributions of wheat lines, testers and their crosses for 7 physiological and morphological traits (Table 6), lines were more prominent and important for characters such as plant height and flag leaf area under normal irrigation, indicating a predominant maternal influence while the contribution of testers were higher for stomatal frequency, stomatal size, epidermal cell size and grain yield per plant, showing a stronger paternal influence. The line × tester interaction contributed predominantly to leaf venation only under normal irrigation. Under water stress, the greatest proportional contribution of lines, testers and their interactions were by lines for flag leaf area, epidermal cell size, leaf venation and grain yield while the contribution by testers was highest for stomatal frequency and stomatal size. Lines × testers contributed predominantly to plant height only under water stress.

## DISCUSSION

Water is a crucial variable in plant growth, and to increase productivity, to sustain physiological processes and to regulate gaseous exchange, stomata and leaf-related traits have prime importance (Maghsoudi and Maghsoudi, 2008; Martiniello and Teixeira da Silva, 2011). Photosynthesis depends primarily upon flag leaf area. Significant differences in different traits under irrigated and water stress conditions, as observed in this study, enhance the chances of selection (Kamaluddin *et al.,* 2007). Genotypes preserving the best ability to regulate stomatal movement may have the best chance of survival under a period of water stress. To better cope with water stress, stomatal frequency, size, and opening and closing behavior minimize water use by leaves (Kim *et al.,* 2004; Ainsworth and Rogers, 2007). Similar selection and variation for stomatal characteristics in wheat was reported by Singh and Sethi (1995) and Mohammady (2002). Shorter plants contribute to yield (Naskidashvili *et al.,*2012), fertilizer responsiveness and the ability to withstand the hazards of high winds and water stress. Positive effects for flag leaf area (Saleh, 2011a) and leaf venation support maximum photosynthesis while negative effects for stomata size and epidermal cell size are important to regulate and tolerate water stress in wheat (Munir *et al.,* 2006; Khan *et al.,* 2010; Saleh, 2011b), a similar trend as found in our study (Table 3). It was evident that under normal irrigation, the negative SCA to GCA ($\sigma^2$sca/$\sigma^2$gca) ratio, along with the degree of dominance ($\sigma^2$D/$\sigma^2$A)$^{1/2}$, being less than 1 for plant height, stomatal frequency,

**Table 5. Estimates of variance of GCA ($\sigma^2$gca) and SCA ($\sigma^2$sca), ratio of SCA to GCA ($\sigma^2$sca/$\sigma^2$gca) and degree of dominance ($\sigma$2D/$\sigma$2A) $^{1/2}$ phenotypic variance ($\sigma^2$p) and genotypic variance ($\sigma^2$g), broad sense heritability along with standard errors ($h^2$BS±SE) among wheat genotypes under normal irrigation and water stress**

| Traits | $\sigma^2_{Gca}$ | | $\sigma^2_{SCa}$ | | ($\sigma^2_{sca}$/ $\sigma^2_{gca}$) | | ($\sigma^2_D$/ $\sigma^2_A$)$^{1/2}$ | | $\sigma^2_P$ | | $\sigma^2_g$ | | $h^2_{BS}$±SE | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | S | N | S | N | S | N | S | N | S | N | S | N | S |
| PH | 0.62 | 1.565 | -6.49 | 7.300 | -10.39 | 4.666 | 0.00 | 2.16 | 47.07 | 66.138 | 21.48 | 51.171 | 0.456±0.11 | 0.773±0.15 |
| FLA | 0.25 | 0.089 | 1.94 | -0.377 | 7.62 | -4.215 | 2.76 | 0.00 | 16.83 | 6.580 | 8.27 | 4.168 | 0.491±0.11 | 0.633±0.13 |
| SF | 1.67 | 1.493 | -3.99 | -2.849 | -2.38 | -1.908 | 0.00 | 0.00 | 56.33 | 70.928 | 40.12 | 54.961 | 0.712±0.14 | 0.774±0.15 |
| SS | 180.92 | 109.648 | -941.70 | -451.34 | -5.20 | -4.116 | 0.00 | 0.00 | 7389.52 | 5316.44 | 3780.1 | 3170.8 | 0.511±0.12 | 0.596±0.13 |
| ECS | 2120.68 | 758.641 | -2275.4 | -9284 | -10.73 | -12.237 | 0.00 | 0.00 | 621238 | 351088 | 465764 | 276248 | 0.749±0.14 | 0.786±0.15 |
| LV | 0.001 | 0.015 | 0.10 | -0.038 | 146.01 | -2.471 | 12.08 | 0.00 | 0.48 | 0.877 | 0.097 | 0.492 | 0.204±0.08 | 0.561±0.12 |
| GY | 0.39 | 0.203 | 2.75 | 2.767 | 8.13 | 13.641 | 2.85 | 3.69 | 16.17 | 10.886 | 10.46 | 9.087 | 0.647±0.13 | 0.834±0.15 |

GCA ($\sigma^2$gca) = variances due to general combining ability. SCA ($\sigma^2$sca) = variances due to specific combining ability

**Table 6. Proportional contribution of 7 lines, 7 testers and their 49 crosses in wheat under normal irrigation and water stress**

| Crosses | PH | | FLA | | SF | | SS | | ECS | | LV | | GY | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | S | N | S | N | S | N | S | N | S | N | S | N | S |
| Lines | 55 | 30 | 44 | 81 | 46 | 46 | 43 | 10 | 8 | 79 | 10 | 48 | 34 | 40 |
| Testers | 35 | 16 | 20 | 5 | 51 | 49 | 52 | 82 | 62 | 4 | 19 | 32 | 36 | 27 |
| L×T | 10 | 54 | 36 | 14 | 3 | 5 | 5 | 8 | 30 | 17 | 71 | 20 | 30 | 33 |

N = normal, S = water stressed, PH = plant height (cm), FLA = flag leaf area ($cm^2$), SF = stomatal frequency, SS = stomatal size ($\mu m^2$), ECS = epidermal cell size ($\mu m^2$), LV = leaf venation, GY = grain yield (g), L×T = line × tester interaction stomatal size and epidermal cell size, revealed additive gene action in these traits. In contrast, flag leaf area, leaf venation and grain yield showed higher values of SCA (i.e., genetic effects) and the $\sigma^2$sca/$\sigma^2$gca ratio was positive, with a degree of dominance greater than 1, revealing a non-additive type of gene action (Table 5). Under water stress, the negative SCA to GCA ($\sigma^2$sca/$\sigma^2$gca) ratio, along with the degree of dominance $(\sigma^2D/\sigma^2A)^{1/2}$, being less than 1, was revealed by flag leaf area, stomatal frequency, stomatal size, epidermal cell size and leaf venation, showing an additive type of gene action. However, plant height and grain yield showed a non-additive type of gene action (Table 5). Higher GCA values have been reported for plant height in wheat (Siddique *et al.,* 2004; Inamullah *et al.,* 2005) although Kashif and Khaliq (2003) indicated that both additive and non-additive genetic effects contributed to plant height in wheat. For flag leaf area in wheat, an additive type of gene action was reported (Ali and Khan, 1998; Khan *et al.,* 2010) while a non-additive gene action in wheat was reportedly essential (Bakhsh *et al.,* 2004). Stomatal frequency showed a minimum degree of dominance under normal and water stress conditions (Table 5), also shown in wheat by Subhani and Chowdhry (2000), although Khan and Rizwan (2000) reported a non-additive gene action for this trait. Lu and Myers (2011) reported both additive and non-additive types of gene action for yield-related traits in cotton. Varieties having smaller stomata performed better under water stress than those with larger stomata (Table 3, 4), as also reported in wheat by Chakalova *et al.* (1980). Stomatal size and frequency are used as morphological markers to identify ploidy level and water stress in many plant species (Beck *et al.,* 2003; Kharazian, 2007). Aryavand *et al.* (2003) and Khazaei *et al.* (2010) revealed significant variation for stomatal frequency between ploidy levels for flag leaves in *Aegilops neglecta* and *Triticum*, respectively. Physiological and morphological traits such as the photoperiodic response during the flowering adaptation of wheat and to mitigate water stress and switch on reproductive growth under changing climatic conditions are genetically controlled (Worland and Snape, 2001) by allelic variation at the *Ppd-A1*, *Ppd-B1* and *Ppd-D1* loci present on homologous group 2 chromosomes (Snape *et al.,* 2001). Wheat breeders always do their best to augment the genetic architecture to increase yield potential even under stressed and non-stressed conditions (Araus *et al.,* 2008; Khan *et al.,* 2010). Similarly, others (Iqbal *et al.,* 2007; Jatoi *et al.,* 2012) found substantial variance in both GCA and SCA for grain yield and related traits in wheat and also reported that GCA variance was more prominent than SCA variance under water stress. However, others (Chowdhry *et al.,* 1999; Arshad and Chowdhry, 2003; Noorka *et al.,* 2007; Saleh, 2011b) found an interactive situation in wheat, reporting a shift in gene action with a change in water availability (Braun *et al.,* 2006). However, temporary and extended drought is the most common yield-limiting factor in a wheat improvement programme. Molecular-assisted selection is necessary to combat drought and to improve grain yield (Quarrie, 1996; Ribaut and Ragot, 2007). The detection of a quantitative trait locus (QTL) is considered to be the initial step in identifying the genomic structural aspect taking part in the control of a quantitative trait (Quarrie, 1999). The physical distance, the precise location of a gene, the size of the QTL effect and saturation level varies in relation to genome size of the crop (Prioul *et al.,* 1997). Heritability estimates, which are determined as the extent of a phenotype, are determined by its genetic makeup or genotypic response although heritability does not depend only upon genetic factors but also on environmental conditions to which an individual is exposed (Falconer, 1970). Heritability estimates in a broad sense were significant for all characters and higher than twice the respective standard error (Table 5). The present study revealed a high level of heritability for flag leaf area, stomatal frequency, stomatal size, and epidermal cell size, ranging between 49 and 100% under normal irrigation but between 56 and 98% under water stress (Table 5). High broad-sense heritability estimates in wheat indicated a preponderance of additive variation in total genetic variability, medium to low heritability suggesting that environmental effects accounted for a major portion of total phenotypic variation (Farshadfar *et al.,* 2000; Ahmed *et al.,* 2007; Khalil *et al.,* 2010; Manes *et al.,* 2012; Noorka *et al.,* 2012). Due to the polygenic nature and substantial influence of environmental conditions, grain yield in wheat is generally characterized by a high genotype × environment interaction and usually shows low heritability (Kearsey and Pooni, 1996; De Vita, 2007; Dodig *et al.,* 2010).

This thus suggests that plant traits associated with water stress tolerance and that have high ranges of heritability with additive genetic effects would be selected at an earlier stage of the breeding program to overcome water stress.

Under normal irrigation and water stress conditions, the proportional contribution of lines, testers and their interactions was altered which shows the effect of water stress on the physiological traits under study. In our study, the lines showed the best proportion for flag leaf area, epidermal cell size, leaf venation and grain yield while testers actively took part in stomatal frequency and stomatal size (Blake *et al*., 2007). However, the line × tester interaction was only best for plant height under water stress. This proportional contribution indicates that lines showed maternal effects which should be used in further breeding programs to allow for crop improvement, and *vice versa*. Different studies have shown that the proportional contribution by lines, testers and their interaction changed for different traits and environmental conditions (Sarker *et al.,* 2002; Rashid *et al.,* 2007) in rice (Shams *et al.,* 2010) and in maize and ryegrass (Tomazewski *et al.,* 2012).

Thus, the present study on combining ability revealed good combiners such as Nesser, Dharwar Dry, Inqilab-91, Chakwal-86, Bakhar2002, 9316, 9252, 9021, 9267, 9247, 9258, as well as promising cross combinations Bakhar-2002 × 9247, Dharwar Dry × 9021, Bakhar-2002 × 9244, Nesser × 9244, GA-2002 × 9252, Kohsitan-97 × 9252, Bakhar 2002 × 9021, Kohistan-97 × 9267, GA-2002 × 9316, Kohistan-97 × 9316, Dharwar Dry × 9021, Kohistan-97 × 9244, Dharwar Dry × 9267, and Bakhar-2002 × 9258, depicting both additive and non-additive variance for multiple traits under both normal irrigation and water stress. All traits discussed displayed both positive and negative values, as well as additive and non-additive gene action paving the path to yield-contributing traits to attain the ultimate goal of breeding, i.e. grain yield (Manès *et al*., 2012). The same best combiners behaved diversely for different traits under normal irrigation and water stress. Regarding grain yield, 9252 (normal) and Dharwar Dry (water stress) performed best overall, although, among testers, 9252 performed equally well. When lines were crossed with the testers, the cross combinations of Dharwar Dry × 9267 and Bakhar-2002 × 9258 attained maximum yield in normal and water stressed conditions, respectively. This indicates that not only is grain yield involved but that yield-contributing traits with most favorable genes may combine in a cross combination allowing them to survive best under both normal and water stressed conditions in the same way that the nature of gene action also shifts with the provision of water. This study concludes that day-to-day water provision for agricultural crops are minimizing, due to continuous changes in climatic conditions. Genotypes and cross combinations need to be screened to be exploited following appropriate breeding procedures to overcome water shortage situations in the world's arid environments. Some good cross combinations in this study showed a shift in gene action, allowing for future research on physico-morphological studies to contribute to the construction of water stress-tolerant wheat genotypes. Further, based on our results, the nature and magnitude of gene action, combining ability, good GCA and SCA effects and their proportional contribution has an ample scope of potential transgressive segregants in segregating generations.

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