*Article*

# Combining Ability of Drought-Tolerant Bread Wheat Genotypes for Agronomic and Physiological Traits

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**Abstract:** A combining-ability analysis is key to select desirable parents and progenies with enhanced response to selection under water-limited environments. The objective of this study was to determine combining ability for agronomic and physiological traits among distantly related drought-tolerant bread wheat (*Triticum aestivum* L.) genotypes under well-watered (WW) and terminal-drought (TD) conditions to determine their genetic merit for breeding. Ten heat- and drought-tolerant wheat genotypes were crossed in a half-diallel mating design to generate 45 $F_1$s, which were evaluated under WW and TD moisture regimes in rainout shelter (RS) and greenhouse (GH) environments. The following agronomic traits were assessed: days to 50% maturity (DTM), plant height (PH), spike length (SL), number of productive tillers (TN), spikelets number per spike (SPS), number of grains per spike (GPS), grain yield (GY) and thousand-kernel weight (TKW); and physiological traits (stomatal conductance (SC) and chlorophyll content index (CCI)). Variances attributable to general combining ability (GCA) and specific combining ability (SCA) were significant ($p < 0.05$) for GY, DTM, PH, SL, SPS, GPS, TKW and CCI. The parental genotypes LM72, LM81 and LM95 with positive and significant GCA effects on GY were selected to make crosses to develop high-yielding wheat genotypes for water-limited environments. Crosses LM71 × LM02, LM71 × LM81, LM82 × LM02, LM82 × LM81, LM22 × LM100, LM22 × LM81 and LM95 × LM22 were selected with positive and significant SCA effects for GY. The selected parents and crosses are valuable genetic resources for breeding and genetic advancement.

**Keywords:** abiotic stress; combining ability; gene action; wheat; yield components; yield gains

## 1. Introduction

Bread wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is the most widely cultivated cereal crop globally [1]. Wheat is a source of essential macro- and micro-nutrients and protein (~14%) [2,3]. A large area of wheat is cultivated under dryland conditions, where drought and heat stresses result in low productivity [4–6].

Hence, a dedicated wheat breeding program is essential to develop high-yielding and well-adapted genotypes possessing yield-promoting agronomic and physiological traits, combining tolerance to abiotic stresses (i.e., heat and drought). Targeted selection for agronomic traits, such as number of days to heading, number of days to maturity, plant height, spike length, number of productive tillers, number of spikelets per spike, number of grains per spike, grain yield and thousand-kernel weight, resulted in yield gains [5,7]. Furthermore, physiological attributes, such as enhanced photosynthetic capacity and stomatal regulation, chlorophyll content of the flag leaves and canopy temperature, are important yield-influencing traits targeted in wheat-improvement programs for maximizing yield

output [8,9]. It is vital to identify germplasm sources for strategic crossing to improve agronomic and physiological yield components that enhance yield potential.

Progeny testing or combining ability analysis by using diallel mating designs has proven to be useful for selecting and identifying wheat parents and progenies possessing desired yield-enhancing traits [10,11]. The general combining ability (GCA) effect is predominantly conditioned by additive gene action, whereas specific combining ability (SCA) provides information about intra- and inter-allelic gene interactions [12]. Despite breeding activities to improve yield potential through the development of high-yielding wheat genotypes for production in drought-stricken regions, yield levels are low and stagnant in most wheat-producing regions, partly because of a poor combination of desired yield-enhancing traits [8,13,14]. Additionally, low yield gains are associated with poor adaptation and susceptibility to the prevailing drought and heat stresses [15].

To improve selection gains for yield under the South African dryland agroecosystems, a phenotypically and genetically diverse population of 100 drought- and heat-adapted wheat genotypes was obtained from CIMMYT's breeding program. From this population, 10 distantly related heat- and drought-adapted and high-yielding wheat genotypes, possessing desired agronomic, physiological and nutritional attributes, were identified for progeny development and strategic selection. A combining-ability analysis of the newly selected parental genotypes and their progenies for yield-enhancing traits is helpful to identify and select promising families for genetic advancement. Thus, the objective of this study was to determine the combining ability for agronomic and physiological traits among drought-tolerant bread wheat genotypes under irrigated and terminal-drought conditions to determine their genetic worth for breeding.

## 2. Materials and Methods

### 2.1. Parental Lines, Crosses and Trial Design

Ten bread wheat genotypes acquired from CIMMYT were used for the study. Information on parental genotypes and pedigrees is presented in Supplementary Table S1. A $10 \times 10$ half-diallel design was used to develop 45 $F_1$ progenies in a greenhouse at the Controlled Environment Facility (CEF) ($29°36'$ S, $30°23'$ E) of the University of KwaZulu-Natal. The parents and progenies were evaluated simultaneously under greenhouse (GH) and rainout shelter (RS) test conditions. Diurnal and nocturnal air temperatures in the greenhouse were set at 31 °C and 16 °C, respectively, and relative humidity ranged between 45% and 55%. The RS environment mimicked field growing conditions, while excluding incoming rainfall. The parents were included to assess their per se performance and as comparative controls. The 10 parental genotypes and 45 $F_1$s were evaluated under irrigated (WW) and terminal drought-stress (TD) moisture regimes under GH and RS test conditions, using a $11 \times 5$ alpha-lattice experimental design, with two replications. The two water regimes and two test conditions provided four test environments for the study, namely WW in GH (Environment 1), TD in GH (Environment 2), WW in RS (Environment 3) and TD in RS conditions (Environment 4). Because of the high number of test genotypes and incomplete blocks involved in an alpha lattice design, the available space was limited, and we only used two replications. Ten-liter capacity polyethylene pots were used for planting in both test conditions. Four pots were allocated per genotype, and five plants were established per pot. Drip irrigation was used to maintain the moisture content of the irrigated treatment at ~70% (i.e., field capacity) until maturity. Moisture level was monitored by using the Hydro Sense II Handheld Soil Moisture Sensor (Campbell Scientific, Somerset West, Western Cape Province, South Africa). To simulate TD conditions, irrigation was withdrawn after 50% of the plants had flowered till maturity.

### 2.2. Data Collection

Data were collected on the following agronomic and physiological traits: days to 50% maturity (DTM) counted from sowing to the day when the stems of the plants appeared golden yellow; plant height (PH) in cm, measured from the base of the plant to the tip of the

spike excluding awns; the number of productive tillers per plant (TN), which were counted at physiological maturity; the number of grains per spike (GPS) were counted per plant; and spike length (SL) in cm. Grain yield (GY) in grams per pot was calculated (the area of the pot was = 0.064 m$^2$). Thereafter, grain yield in grams/m$^2$ was extrapolated to grain yield in tons/ha. Thousand-kernel weight (TKW) in grams was determined from randomly sampled 1000 seeds after harvest and expressed as g/1000 seed. Stomatal conductance (SC) in mmol m$^{-2}$ s$^{-1}$ and chlorophyll content index (CCI) were also determined. Stomatal conductance was recorded from the upper surface of the flag leaf, using the SC-1 Leaf Porometer (Decagon Devices Inc., Pullman, WA, USA), between 10 a.m. and 12 noon, under sunny skies. Leaf chlorophyll content index was measured from the upper surface of healthy fully opened flag leaves, using a chlorophyll meter (CCM 200 plus Opti-Sciences, Hudson, NY, USA). DTM, PH, TN, GPS, SL, GY and TKW were measured from five plants per replication, whereas SC and CCI were measured from flag leaves of three plants per replication.

*2.3. Data Analysis*
2.3.1. Analysis of Variance

Analysis of variance was performed by using Genstat v18 [16]. The least significant difference (LSD) was computed to compare treatment means at 5% probability level.

2.3.2. Assessment of GCA and SCA Effects

Mean performances data averaged across replications were used to determine magnitudes of GCA and SCA effects across the four environments, and separately for WW and TD under RS and GH, using Griffing's Method IV (F$_1$s only) (Griffing 1956). The parents were initially selected from a pool of genetically diverse genotypes. The F$_1$s were considered a fixed effect, whereas the test environments were treated as a random effect. As a result, Griffing's Model I (fixed effects) was employed to estimate GCA and SCA effects. The analysis was performed by using AGD-R (Analysis of Genetic Designs in R) v5.0 [17], using the following fixed-effect model:

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$$

where $Y_{ijk}$ is the recorded value for the *ij*th cross in the *k*th replication, $\mu$ is the population mean, $g_i$ and $g_j$ are the GCA effects for the *i*th and *j*th parents, $s_{ij}$ the SCA effect and $e_{ijk}$ the error term associated with the *ij*th cross in the *k*th replication. The significance of the GCA and SCA effects for the assessed traits was computed by using a *t*-test at 5% level of significance.

2.3.3. Associations among Agronomic and Physiological Traits

A correlation matrix was computed to establish relationships among assessed agronomic and physiological traits evaluated under irrigated and terminal drought moisture regimes, using SPSS v25 (SPSS Inc., Chicago, IL, USA, 2018). The significance of the correlations for the assessed traits was computed by using a *t*-test at 5% level of significance.

## 3. Results
*3.1. Genotype, Moisture Regime, Testing Environments and Their Interaction Effects*

An analysis of variance showing genotype, moisture regime, test condition and their interaction effects is presented in Table 1. Significant ($p < 0.001$) genotypic effects were observed for all traits, except for TN and SC (Table 1). Moisture regime effects were highly significant ($p < 0.001$) for all traits, except for TN. The test condition significantly ($p < 0.01$) affected the studied traits, except for GPS. Significant ($p < 0.05$) genotype × moisture regime interaction effects were recorded for DTM, SL, GY and SC. Furthermore, significant ($p < 0.001$) genotype × moisture regime × environment interaction effects were detected for DTM and SL.

**Table 1.** Analysis of variance showing mean squares and significant tests for assessed agronomic and physiological traits among 10 wheat parents and their $F_1$ progenies under irrigated (WW) and terminal drought (TD) in rainout shelter (RS) and greenhouse (GH) environments.

| Source of Variation | df | DTM | PH | SL | TN | SPS | GPS | GY | TKW | SC | CCI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Traits † | | | | |
| Block | 1 | 4.81 | 101.78 | 261.38 ** | 0.04 | 8.12 | 23.54 | 1.78 | 0.68 | 20,160.70 ** | 1.11 |
| Incomplete block | 8 | 58.05 ** | 100.78 ** | 7.29 * | 0.57 | 5.54 | 24.52 | 2.41 ** | 18.08 | 1526.40 | 72.68 |
| Gen | 54 | 183.72 ** | 216.77 ** | 26.51 ** | 2.08 | 18.69 ** | 90.93 ** | 2.79 ** | 139.67 ** | 1113.4 | 126.17 ** |
| MR | 1 | 3228.70 ** | 371.03 ** | 932.27 ** | 1.28 | 247.56 ** | 1576.62 ** | 1392.35 ** | 119,111.84 ** | 2,016,389.90 ** | 28,648.92 ** |
| Env | 1 | 7830.62 ** | 2672.32 ** | 19.16 ** | 49.10 ** | 156.51 ** | 30.42 | 14.89 ** | 2275.10 ** | 73,164.30 ** | 9128.04 ** |
| Gen × MR | 54 | 15.14 * | 39.82 | 6.49** | 0.67 | 4.48 | 18.25 | 2.21 ** | 54.61 | 1413.00 ** | 55.53 |
| Gen × TC | 54 | 60.63 ** | 43.93 | 4.58 * | 1.11 | 6.30 | 25.38 | 0.72 | 16.89 | 582.20 | 42.79 |
| MR × TC | 1 | 95.01 ** | 486.68 ** | 222.47 ** | 12.88 ** | 186.45 ** | 114.34 ** | 8.10 ** | 3582.19 * | 43,857.50 ** | 589.02 ** |
| Gen × MR × TC | 54 | 18.76 ** | 40.24 | 7.18 ** | 0.73 | 4.92 | 20.33 | 0.86 | 22.93 | 549.70 | 19.81 |
| Residual | 211 | 10.47 | 39.67 | 3.03 | 1.54 | 5.64 | 22.18 | 0.91 | 39.92 | 828.4 | 70.49 |

Note: df, degrees of freedom; * and ** denote significantly different from zero at 5 and 1% probability levels, respectively. † DTM, number of days to maturity; PH, plant height; SL, spike length; TN, number of productive tillers; SPS, number of spikelets per spike; GPS, grain per spike; GY, grain yield; TKW, thousand-kernel weight; SC, stomatal conductance; CCI, chlorophyll content index; MR, moisture regime (irrigated and drought); Gen, genotype; TC, test condition (glasshouse and rainout shelter).

### 3.2. Performance of Wheat Parents and Progenies for Agronomic and Physiological Traits

Mean performance among parents and progenies for the evaluated traits is presented in Supplementary Tables S2 and S3, respectively. In the present study, the lowest DTM values were recorded for cross LM22 × LM81 in GH (77 days) and RS (91 days) under WW moisture regime (Supplementary Table S2). Under TD, a significantly lower DTM of 83 days was recorded for LM95 × LM100 in the RS environment, whereas 75 days was recorded for the crosses LM02 × LM32 and LM95 × LM81 in the GH environment (Supplementary Table S3).

The plant height of the newly developed $F_1$ progenies varied between 74 and 100 cm (Supplementary Tables S2 and S3). Crosses LM82 × LM81 and LM02 × LM81 recorded the lowest PH of 72.00 and 74.00 cm under the RS and GH environments, respectively, compared to their parental genotypes (i.e., LM02, LM81 and LM82), which recorded between 98 and 101 days (Supplementary Table S2). Under the TD moisture regime, crosses LM82 × LM81 and LM95 × LM44 recorded the lowest PH of 77.00 cm in RS, whereas LM02 × LM81 was identified as having the lowest PH of 71.00 cm under GH. The PH values of these crosses (i.e., LM82 × LM81, LM95 × LM44 and LM02LM81) were lower than the values recorded for their parental genotypes under TD (>88 days) (Supplementary Table S3).

Regarding TKW, the tested wheat lines recorded values ranging from 15 to 46.34 g under drought stress (Supplementary Table S3). The highest TKW was recorded for crosses LM71 × LM81 (71.70 g) in RS under the WW moisture regime, whereas LM71 × LM32 and LM82 × LM71 recorded 70.81 g in the GH environment. The TKW of these crosses is higher than the values (ranging from 54 to 66 g) recorded for parental genotypes LM32, LM81 and LM82 under RS and GH (Supplementary Table S2). Under TD, crosses LM82×LM81 and LM95 × LM32 recorded TKW of 30.93 and 30.27 g, respectively, in the RS environment, whereas LM02 × LM81 and LM71 × LM100 exhibited a TKW of 46.34 and 45.28 g, respectively, in the GH environment (Supplementary Table S3).

The present study identified crosses LM71 × LM81, LM71 × LM44 and LM95 × LM02, LM71 × LM32, LM71 × LM100 and LM82 × LM71 with a yield potential of >9 t ha$^{-1}$ under the WW moisture regime in the RS and GH environments (Supplementary Table S2). Conversely, LM22 × LM81, LM95 × LM100, LM72 × LM44, LM22 × LM22, LM95 × LM02 and LM71 × LM44 recorded a grain yield of >5 t ha$^{-1}$ under terminal drought (Supplementary Table S3).

The crosses LM71 × LM02 and LM71 × LM32 recorded high SC of 74.18 and 73.00 mmol m$^{-2}$ s$^{-1}$, respectively, under TD in the RS environment, whereas LM32 × LM100

and LM82 × LM81 had SC values of 90.42 and 82.48 mmol m$^{-2}$ s$^{-1}$, respectively, in the GH environment (Supplementary Table S3). High chlorophyll content index values of 34.84 and 33.94 were recorded for crosses LM71 × LM32 and LM44 × LM32, respectively, under TD in the RS environment, while crosses LM95 × LM44 and LM32 × LM22 exhibited CCI values of 16.00 and 21.18 in the GH environment, respectively.

### 3.3. Combining Ability Analysis of Parents and F$_1$ Progenies

Mean squares and significant tests for GCA and SCA effects for the assessed traits across test environments are presented in Table 2. The GCA was significant for DTM, PH, SL, SPS, GPS, GY, TKW and CCI, whereas the SCA was significant for all traits. The GCA × environment effect was significant for DTM and SL, whereas the SCA × environment interaction effect was significant for SL and GY.

**Table 2.** Mean squares and significant tests for GCA and SCA effects for assessed agronomic and physiological traits † among 10 wheat parents and their progenies across four environments.

| Source of Variation | df | Traits † | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | DTM | PH | SL | TN | SPS | GPS | GY | TKW | SC | CCI |
| Environment (E) | 3 | 4616.70 ** | 872.84 ** | 323.58 ** | 15.39 ** | 160.93 ** | 462.95 ** | 380.65 ** | 34,439.34 ** | 568,016.80 ** | 10,777.64 ** |
| Reps | 4 | 30.10 ** | 229.72 ** | 63.87 ** | 7.41 ** | 7.85 ** | 33.41 ** | 4.72 ** | 78.58 ** | 8248.25 ** | 304.50 ** |
| Genotype (G) | 44 | 54.20 ** | 244.13 ** | 29.01 ** | 1.89 ** | 17.48 ** | 52.67 ** | 2.79 ** | 147.93 ** | 1278.69 * | 114.83 ** |
| GCA ‡ | 9 | 70.64 ** | 365.01 ** | 31.81 ** | 0.69 | 19.91 ** | 58.87 ** | 3.65 ** | 137.44 ** | 847.70 | 146.18 ** |
| SCA § | 35 | 49.97 ** | 213.04 ** | 28.29 ** | 2.20 * | 16.85 ** | 51.08 ** | 2.57 ** | 150.63 ** | 1389.51 * | 106.77 ** |
| G × E | 132 | 13.63 ** | 46.61 | 6.05 | 0.79 | 4.79 | 21.18 | 1.21 | 33.83 | 865.89 | 45.60 |
| GCA × Env | 27 | 17.77 ** | 34.86 | 5.79 ** | 042 | 3.37 | 17.71 | 1.34 | 27.95 | 899.53 | 30.52 |
| SCA × Env | 105 | 12.57 * | 48.87 | 6.12 ** | 0.89 | 5.16 | 22.07 | 1.18 | 35.34 | 857.23 | 49.48 |
| Residual | 96 | 8.79 | 37.84 | 2.83 | 1.38 | 4.41 | 21.39 | 0.86 | 39.32 | 791.12 | 58.74 |

Notes: * and ** denote significantly different from zero at 5% and 1% probability level, respectively. † DTM, number of days to maturity; PH, plant height; SL, spike length; TN, number of productive tillers; SPS, number of spikelets per spike; GPS, grain per spike; GY, grain yield; TKW, thousand-kernel weight; SC, stomatal conductance; CCI, chlorophyll content index; E, environments (i.e., WW in GH, TD in GH, WW in RS, TD in RS). ‡ GCA, general combining ability. § SCA, specific combining ability.

### 3.3.1. General Combining Ability Effects of Parental Genotypes

The GCA effects of parental wheat genotypes under WW and TD conditions in the RS and GH environments are presented in Table 3. Regarding DTM, negative and significant ($p < 0.05$) GCA effect was recorded for parental genotype LM44 under WW in the RS environment, whereas LM82 recorded the highest negative and significant ($p < 0.01$) SCA effect under RS. Under TD, the highest negative and significant ($p < 0.05$) GCA effect for DTM was recorded for parents LM81 and LM32 in the RS and GH environments, respectively. The highest negative and significant ($p < 0.01$) GCA effect for PH was recorded for parental genotype LM82 under WW in the RS and GH environments, whereas LM22 andLM82 were identified as having the highest negative and significant ($p < 0.01$) GCA under TD in the RS and GH environments, respectively. Parental genotypes LM02 and LM71 recorded the highest positive GCA effects for SL under WW in the RS and GH environments, in that order. Regarding SPS, positive and significant ($p < 0.01$) GCA effects were recorded for parents LM44 and LM72 under WW in the RS and GH environments, respectively. The GCA effect for SPS was positive and significant for parental genotype LM72 under TD in the RS and GH environments. Parent LM44 recorded a high positive and significant ($p < 0.05$) GCA effect for GPS under WW in the RS and GH environments and under TD in the RS environment. Parental genotype LM95 recorded a positive and significant ($p < 0.01$) GCA effect for GY under WW in the RS and GH environments, whereas LM72 and LM95 showed positive and significant GCA effects under TD in the RS and GH environments, respectively. For TKW, parent LM95 recorded a positive and significant ($p < 0.01$) GCA effect under WW in the RS and GH environments, whereas LM22 and LM95 were identified as having positive and significant ($p < 0.05$) GCA effects under TD in the

GH environment. Genotype LM22 was identified as having a positive and significant GCA effect for CCI under WW in the GH environment.

**Table 3.** General combining ability effects for studied agronomic and physiological traits among 10 parental bread wheat genotypes of bread wheat evaluated under irrigated and terminal drought conditions in rainout shelter (RS) and glasshouse (GH) environments.

| Traits † | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DTM | | PH | | SL | | TN | | SPS | | GPS | | GY | |
| Parents | RS | GH | RS | GH | RS | GH | RS | GH | RS | GH | RS | GH | RS | GH |
| Irrigated | | | | | | | | | | | | | | |
| LM02 | −0.04 | −0.30 | 2.73 * | 1.74 | 0.85 ** | 0.41 | −0.14 | 0.15 | 0.07 | 0.18 | −0.28 | −0.07 | 0.28 | 0.24 |
| LM22 | −0.48 | −0.55 | −2.61 * | −3.75 ** | −0.43 * | −0.63 | 0.04 | −0.17 | −0.24 | −0.31 | 0.11 | −0.21 | 0.05 | 0.25 |
| LM32 | −0.66 | −1.24 * | 1.31 | 2.01 * | 0.48 * | 1.00 ** | 0.20 | 0.12 | −0.46 | 0.02 | −1.50 | 0.19 | −0.13 | −0.10 |
| LM44 | −0.91* | −0.61 | 2.04 | 2.98 ** | −0.52 * | −0.98 ** | 0.07 | 0.04 | 1.27 ** | 0.75 | 1.96 * | 1.83 * | −0.23 | 0.39 |
| LM71 | −0.66 | 0.51 | −0.13 | −0.30 | −0.92** | −0.93 ** | −0.09 | −0.04 | 0.36 | 0.04 | 1.22 | 0.92 | −0.18 | −0.70** |
| LM72 | 2.15 ** | 1.95 ** | 0.58 | 1.28 | 1.82 ** | 1.72 ** | 0.04 | 0.12 | 0.49 | 1.08 ** | 0.39 | 1.89 * | −0.06 | 0.05 |
| LM81 | 0.03 | −1.18 * | 4.31 ** | 4.24 ** | −0.19 | −0.05 | −0.14 | −0.34 | 0.08 | 0.21 | 1.36 | −0.28 | 0.31 * | −0.09 |
| LM82 | 1.09 ** | 2.20 ** | −3.51 ** | −4.19 ** | −0.67 ** | −0.71 ** | 0.12 | 0.09 | −0.18 | −1.00 ** | −1.32 | −2.18 * | −0.44 ** | −0.10 |
| LM95 | −0.60 | −0.80 | −1.74 | −1.19 | 0.28 | 0.33 | −0.21 | 0.00 | −1.21 ** | −0.95 * | −1.23 | −1.91 * | 0.68 ** | 1.18 ** |
| LM100 | 0.09 | 0.01 | −2.99 * | −2.81 ** | −0.71 ** | −0.17 | 0.11 | 0.04 | −0.19 | −0.02 | −0.73 | −0.18 | −0.28 | −0.33 |
| Terminal drought | | | | | | | | | | | | | | |
| LM02 | −2.31 ** | 0.23 | −1.84 | 2.97 ** | −1.31 ** | 0.56 | 0.05 | −0.12 | −1.36 ** | 0.15 | −1.07 | −0.45 | 0.02 | −0.03 |
| LM22 | 1.06 | −0.78 | −4.15 ** | −3.63 ** | −0.73 * | −0.92 * | 0.07 | −0.08 | −0.66 | −0.12 | −1.39 | 2.53 ** | 0.25 | −0.11 |
| LM32 | 1.44 * | −1.71 * | 2.21 | 1.73* | −0.08 | 0.97 * | −0.09 | 0.13 | −0.62 | −0.12 | −0.47 | −0.35 | 0.26 | −0.07 |
| LM44 | 1.31 * | −0.78 | 3.86 ** | 2.59 ** | 0.18 | −0.42 | 0.11 | 0.49 | 0.20 | 0.85 * | 2.39 ** | 0.32 | −0.23 | 0.11 |
| LM71 | 0.63 | 0.60 | 0.77 | 0.42 | 0.64 * | −0.59 | −0.03 | 0.07 | 0.54 | −0.19 | 1.11 | 0.87 | −0.25 | 0.08 |
| LM72 | 0.88 | 1.91 ** | −2.54 | 1.82 * | 0.96 ** | 2.10 ** | 0.00 | 0.00 | 1.57 ** | 0.97 * | 0.30 | 0.57 | 0.38 * | −0.04 |
| LM81 | −4.13 ** | −1.40 * | 0.94 | 3.14 ** | −0.37 | −0.03 | −0.16 | −0.06 | −0.11 | −0.02 | −1.32 | −0.32 | −0.10 | −0.04 |
| LM82 | 0.81 | 2.73 ** | −0.59 | −4.53 ** | 0.92 ** | 0.04 | 0.12 | −0.14 | −0.45 | −0.91 * | 0.22 | −0.41 | 0.03 | −0.22 |
| LM95 | 0.06 | −1.21 | 0.10 | −0.94 | 0.29 | −0.31 | 0.14 | −0.49 | 0.18 | −0.67 | 0.30 | −3.50 ** | −0.30* | 0.58 ** |
| LM100 | 0.25 | 0.41 | 1.24 | −3.58 ** | −0.49 | −1.40 ** | −0.21 | 0.19 | 0.71 | 0.06 | −0.07 | 0.75 | −0.05 | −0.26 |

| | TKW | | SC | | CCI | |
|---|---|---|---|---|---|---|
| Parents | RS | GH | RS | GH | RS | GH |
| Irrigated | | | | | | |
| LM02 | −1.31 | −1.26 | 7.64 * | −8.41 | −3.01 | −4.09 * |
| LM22 | 1.33 | 0.98 | −6.45 | 13.60 | 3.04 | 4.50 * |
| LM32 | 2.27 | 2.11 | −3.79 | −7.42 | 0.00 | −1.17 |
| LM44 | −1.21 | −1.25 | 8.66 * | 19.31 * | 0.58 | 1.04 |
| LM71 | −3.00 * | −2.59 | −2.24 | −21.43 * | 1.12 | 0.45 |
| LM72 | 1.05 | 1.82 | 6.54 | 12.82 | 0.89 | 2.45 |
| LM81 | −0.09 | −1.51 | −3.31 | 4.97 | −1.66 | 1.19 |
| LM82 | −2.80 * | −2.55 | 0.73 | −5.39 | 1.47 | −0.70 |
| LM95 | 4.48 ** | 3.96 ** | −8.17 * | −2.18 | 1.74 | −0.06 |
| LM100 | −0.71 | 0.30 | 0.38 | −5.88 | −4.18 * | −3.61 |
| Terminal drought | | | | | | |
| LM02 | 0.12 | −0.84 | 4.74 | 5.31 ** | 1.26 | −0.86 |
| LM22 | 0.49 | 3.16 ** | −0.63 | −1.77 | 2.02 | 0.74 |
| LM32 | −0.87 | 0.46 | −2.52 | −8.89 ** | −1.51 | 0.17 |
| LM44 | −0.23 | −1.58 | −3.95 | −0.90 | 1.42 | 0.17 |
| LM71 | 0.30 | −1.77 | 3.44 | 7.52 ** | 0.73 | 1.26 |
| LM72 | 0.54 | −1.54 | 2.50 | −2.40 | 0.90 | 0.32 |
| LM81 | 0.03 | 1.48 | 0.49 | 0.59 | −0.07 | −0.52 |
| LM82 | −0.04 | −1.53 | −2.51 | −1.82 | −0.02 | −0.06 |
| LM95 | 0.07 | 2.70 * | 0.44 | 4.75 ** | −2.40 | −0.14 |
| LM100 | −0.41 | −0.53 | −2.01 | −2.38 | −2.32 | −1.08 |

Notes: * and ** denote significantly different from zero at 5% and 1% probability level of a *t*-test statistic, respectively. † DTM, number of days to maturity; PH, plant height; SL, spike length; TN, number of productive tillers; SPS, number of spikelets per spike; GPS, grain per spike; GY, grain yield; TKW, thousand-kernel weight; SC, stomatal conductance; CCI, chlorophyll content index.

### 3.3.2. Specific Combining Ability Effects of F$_1$ Progenies

The SCA effects of crosses for assessed agronomic and physiological traits under WW and TD conditions in the RS and GH environments are presented in Supplementary Tables S4 and S5, respectively. Cross LM32 × LM81 displayed the highest negative and significant ($p < 0.05$) SCA effect for DTM under WW in the RS and GH environments, whereas LM32 × LM81 recorded the highest negative and significant ($p < 0.01$) SCA effects under TD condition. Crosses LM44 × LM100, LM72 × LM22, LM95 × LM32, LM95 × LM44 and LM95 × LM81 recorded negative and significant ($p < 0.05$) SCA effects for PH under WW condition in the RS and GH environments. Under TD, the highest negative

and significant ($p < 0.01$) SCA effects for PH were recorded for crosses LM82 × LM71 and LM44 × LM100 under the RS and GH environments, respectively. For TN, cross LM72 × LM02 and LM82 × LM22 recorded the highest positive and significant ($p < 0.01$) SCA effects for TN under WW and TD conditions in the GH environment.

For SPS, crosses LM32 × LM100 and LM82 × LM100 recorded the highest positive and significant ($p < 0.05$) SCA effects under WW conditions, whereas crosses LM95 × LM22 and LM82 × LM100 recorded the highest positive and significant ($p < 0.01$) SCA effects under TD in the RS and GH environments, respectively. The SCA effects were non-significant for GPS for all crosses under WW condition in the RS environment, whereas LM82 × LM100 recorded a positive and significant ($p < 0.51$) SCA effect for GPS under the RS environment. Under TD, LM95 × LM81 and LM44 × LM81 recorded a positive and significant ($p < 0.05$) SCA effect for GPS under TD condition in the GH environment. Crosses LM71 × LM02 and LM82 × LM02 recorded the highest positive and significant ($p < 0.01$) SCA effects for GY under WW in the RS and GH environments. Under TD, LM95 × LM22 and LM82 × LM02 were identified as having the highest positive and significant ($p < 0.01$) SCA effects in the RS and GH environments, respectively. Cross LM82 × LM02 exhibited the highest positive and significant ($p < 0.05$) SCA effect for TKW under WW in the RS and GH environments, whereas the SCA effects for TKW were positive and significant ($p < 0.05$) for LM44 × LM100 and LM71 × LM100 under TD conditions. Regarding SC, LM02 × LM81 and LM81 × LM100 recorded positive and significant ($p < 0.05$) SCA effects under WW in the RS environment, whereas LM71 × LM44 showed the highest positive and significant ($p < 0.05$) SCA effect under TD condition in the RS environment. Crosses LM71 × LM02 and LM95 × LM44 displayed positive and significant ($p < 0.05$) SCA effects for CCI under WW, and LM72 × LM81 and LM71 × LM22 under TD in the RS and GH environments, respectively.

*3.4. Associations among Agronomic and Physiological Traits under Irrigated and Terminal Drought Conditions*

Pearson's correlation coefficients ($r$) showing associations among the studied agronomic and physiological traits under irrigated and terminal drought conditions in the RS and GH environments are presented in Tables 4 and 5, respectively. Significant and positive correlations were observed between SL with SPS ($r = 0.39$; $p \leq 0.05$) and TKW ($r = 0.33$; $p \leq 0.01$) under NS conditions in the RS environment. GPS positively and significantly correlated with SPS ($r = 0.72$; $p \leq 0.01$) under NS conditions in the RS environment. GY was significantly and positively correlated with TKW ($r = 0.68$; $p \leq 0.01$) under NS conditions in the RS environment. Under TD conditions in the RS environment, TKW positively correlated with SL ($r = 0.28$; $p \leq 0.05$), whereas GY positively correlated with CCI ($r = 0.34$; $p \leq 0.05$).

Under the GH environment, significant and positive correlations were observed between PH with SPS ($r = 0.39$; $p \leq 0.05$) and GPS ($r = 0.32$; $p \leq 0.05$) under NS condition. SL positively correlated with TKW ($r = 0.31$; $p \leq 0.05$), whereas GPS positively and significantly correlated with SPS ($r = 0.95$; $p \leq 0.001$) under NS conditions in the GH environment. GY positively and significantly correlated with TKW ($r = 0.58$; $p \leq 0.01$) under NS conditions in the GH environment. GY positively correlated with SC ($r = 0.52$; $p \leq 0.05$) under DS conditions in the GH environment.

**Table 4.** Pearson correlation coefficients showing associations between assessed agronomic and physiological traits among 10 wheat parental genotypes and crosses under irrigated (lower diagonal) and terminal drought (upper diagonal) in the RS environment.

| Traits † | DTM | PH | SL | TN | SPS | GPS | GY | TKW | SC | CCI |
|---|---|---|---|---|---|---|---|---|---|---|
| DTM | | 0.15 | 0.05 | 0.14 | 0.29 * | 0.11 | −0.13 | −0.05 | −0.16 | 0.02 |
| PH | 0.05 | | 0.20 | −0.01 | 0.30 | 0.05 | −0.03 | −0.16 | −0.30 * | 0.15 |
| SL | 0.08 | 0.14 | | −0.00 | 0.19 | 0.14 | 0.17 | 0.28 * | −0.13 | 0.15 |
| TN | 0.20 | −0.16 | −0.08 | | 0.23 | 0.10 | −0.11 | 0.05 | 0.08 | 0.24 |
| SPS | 0.10 | 0.22 | 0.39 ** | −0.02 | | 0.62 ** | 0.10 | −0.24 | −0.17 | 0.09 |
| GPS | 0.11 | 0.19 | 0.04 | −0.01 | 0.72 ** | | −0.11 | −0.12 | −0.17 | 0.04 |
| GY | −0.05 | 0.02 | 0.16 | −0.10 | −0.04 | 0.01 | | 0.07 | −0.10 | 0.34 * |
| TKW | 0.11 | −0.07 | 0.33 * | −0.04 | −0.04 | −0.19 | 0.68 ** | | −0.10 | 0.18 |
| SC | 0.13 | 0.06 | 0.13 | 0.18 | 0.17 | −0.01 | 0-.20 | −0.18 | | 0.09 |
| CCI | −0.01 | 0.03 | 0.08 | −0.25 | −0.03 | −0.07 | 0.15 | 0.25 | 0.04 | |

Notes: * and ** denote significant at 5 and 1% probability level of *t*-values based on a two-tailed test, respectively. † DTM, number of days to maturity; PH, plant height; SL, spike length; TN, number of productive tillers; SPS, number of spikelets per spike; GPS, grain per spike; GY, grain yield; TKW, thousand-kernel weight; SC, stomatal conductance; CCI, chlorophyll content index.

**Table 5.** Pearson correlation coefficients showing association between studied agronomic and physiological traits among wheat genotypes under irrigated (lower diagonal) and terminal drought (upper diagonal) in the GH environment.

| Traits † | DTM | PH | SL | TN | SPS | GPS | GY | TKW | SC | CCI |
|---|---|---|---|---|---|---|---|---|---|---|
| DTM | | 0.08 | −0.02 | 0.12 | −0.04 | 0.01 | −0.10 | 0.15 | −0.08 | 0.28 * |
| PH | 0.03 | | 0.02 | 0.01 | 0.15 | −0.13 | 0.03 | −0.12 | 0.02 | 0.17 |
| SL | −0.05 | 0.26 | | −0.19 | 0.24 | 0.11 | −0.09 | 0.15 | −0.28 * | −0.03 |
| TN | 0.26 | −0.19 | −0.03 | | −0.01 | 0.11 | −0.05 | 0.19 | 0.09 | 0.12 |
| SPS | 0.04 | 0.39 ** | 0.25 | −0.03 | | 0.72 ** | −0.06 | −0.10 | 0.02 | 0.15 |
| GPS | 0.04 | 0.32 * | 0.19 | −0.03 | 0.95 ** | | −0.10 | 0.06 | −0.10 | 0.11 |
| GY | −0.04 | −0.06 | 0.09 | −0.16 | −0.11 | −0.14 | | 0.02 | 0.52 ** | 0.07 |
| TKW | 0.05 | −0.16 | 0.31 * | −0.10 | −0.17 | −0.08 | 0.58 ** | | −0.11 | −0.03 |
| SC | 0.1 | 0.06 | 0.04 | 0.07 | 0.19 | 0.12 | −0.06 | −0.12 | | 0.01 |
| CCI | 0.18 | 0.14 | −0.05 | −0.16 | 0.12 | 0.11 | 0.05 | −0.04 | 0.19 | |

Notes: * and ** denote significant at 5 and 1% probability level of *t*-values based on a two-tailed test, respectively. † DTM, number of days to maturity; PH, plant height; SL, spike length; TN, number of productive tillers; SPS, number of spikelets per spike; GPS, grain per spike; GY, grain yield; TKW, thousand-kernel weight; SC, stomatal conductance; CCI, chlorophyll content index.

## 4. Discussion

The yield potential of wheat and yield genetic gains are low under water-restricted environments, due to poor selection and development of drought- and heat-adapted genotypes for production. This can be overcome by developing well-adapted and high-yielding wheat genotypes that possess yield-improving agronomic and physiological characteristics. The current study revealed significant genotype effects for assessed traits that are useful for selecting suitable parental genotypes for breeding to develop new crosses for advancement and further selection. The significant genotype-by-environment interaction effect enabled the selection of the best genotypes under the variable test conditions. A significant GCA indicated additive gene action, whereas a significant SCA effect suggested non-additive gene action influencing trait expression. Furthermore, the significant interaction between the environment and GCA and SCA effects suggested that GCA and SCA effects were environment-specific, and that the selection of best genotypes should be undertaken across multiple environments (Tables 2 and 3). Positive GCA and SCA effects for traits, such as number of tillers, number of spikelets per spike, grains per spike, thousand-kernel weight and grain yield, were reported in bread wheat evaluated under drought stress and irrigated conditions [18,19]. The reports suggest the importance of crosses involving contrasting parents to select drought-tolerant wheat genotypes for genetic improvement programs.

The genetic advancement of the newly developed wheat families could be achieved through targeted selection of yield-promoting agronomic and physiological traits that improve yield response, especially under water-limited environments. Early maturity is an important trait targeted in wheat-breeding programs as a drought escape mechanism, and it helps achieve a reasonable yield under post-flowering drought conditions [7,20]. In the present study, the number of days to maturity ranged from 88 to 105 among parental genotypes, and from 83 to 105 for crosses under drought in field conditions (Supplementary Table S3). The low range values for crosses suggest positive genetic improvement for earliness. The poor correlation between days to maturity with grain yield under terminal drought conditions suggested limited yield improvement targeting phenology among the newly developed wheat populations (Tables 4 and 5). Moreover, the number of days to maturity was poorly correlated with other yield-component traits under drought-stress conditions, suggesting limited potential to improve grain yield via indirect selection for phenological response among the $F_1$ progenies. Drought stress occurring during anthesis and grain-filling periods can result in fewer spikelets and kernels per spike and low grain yield [21]. Breeding for early maturity in wheat is a useful drought-avoidance strategy that allows plants to escape terminal drought stress under drought-prone environments. Parental genotypes (i.e., LM02 and LM81) possessing negative GCA effects for days to maturity under stressed field conditions (Table 3) show potential for enhancing earliness in wheat. Furthermore, crosses such as LM44 × LMLM81 and LM71 × LM95, which identified as having high SCA effects for days to maturity under stressed field conditions (Table 3), are potential genetic resources for selection to enhance earliness in wheat. For instance, the cross LM71 × LM95 reached physiological maturity 12 days earlier compared to parental genotypes, such as LM95, which matured at 101 days under stressed field conditions (Supplementary Table S3). This suggests genetic advancement for days to maturity for this cross genotype in $F_1$ generation.

Reduced plant height is associated with high yield potential in wheat by improving lodging resistance and increasing the harvest index [22]. The present study found limited genetic improvement in plant height among the newly developed progenies. For example, heat- and drought-tolerant wheat genotype LM22 with desirable negative GCA effect for plant height resulted in a positive SCA effect for cross LM22 × LM81 progeny under stress field conditions (Tables 4 and 5). The positive SCA values suggest that plant height in LM22 is under paternal control. Conversely, crosses LM71 × LM100 and LM82 × LM71 showed reduced plant height despite the non-significant GCA effects for their parents under stressed field conditions (Table 3). The grain yield of crosses LM71 × LM100 and LM82 × LM71 under stressed field conditions were 4.23 and 3.20 t ha$^{-1}$, respectively, combining short plant height and relatively good yield (Supplementary Table S3). The lack of correlation between plant height and grain yield ($r = -0.03$; $p > 0.05$) under stressed field conditions indicates the need for independent selection of the two traits in the tested wheat lines (Table 5).

Targeted selection for increased thousand-kernel weight is important to improve grain yield potential and genetic gain [5,8]. The tested $F_1$ wheat population showed variation for thousand-kernel weight ranging from 15.07 to 46.34 g under stressed conditions, compared to 43.84–70.70 g under irrigated conditions across the environments (Supplementary Table S3). A range of thousand-kernel weight of 32.19 to 64.31 g was reported by Reference [11] for $F_2$ wheat progenies tested under drought conditions—higher than the values reported in the present study (i.e., 15.07–46.34 g). The lower range of thousand-kernel weight observed among progenies under TD than under WW suggests reduced selection efficiency under stressed growing conditions. As a result, a parental genotype (i.e., LM95) which was identified as having a positive GCA effect for thousand-kernel weight under TD (Table 3) produced a cross (i.e., LM95 × LM02) with a negative and significant SCA effect for TKW under similar a growing condition (Supplementary Table S5). Furthermore, the thousand-kernel weight showed a strong and positive relationship with grain yield only under irrigated moisture regime, suggesting higher selection response under

a non-stress environment (Tables 4 and 5). Breeding progress in wheat, combining both high grain number and thousand-kernel weight, has been limited because of a negative association between these two component traits. The present study revealed low, non-significant correlations between the thousand-kernel weight and number of grains per spike (Tables 4 and 5), hindering the co-selection of the two traits in the studied wheat germplasm at the $F_1$.

The grain yield is an important economic trait that is influenced by several yield components. The present study identified crosses such as LM71 × LM81, LM71 × LM44, LM95 × LM02, LM71 × LM32, LM71 × LM100 and LM82 × LM71 with a high yield potential of >9 t ha$^{-1}$ under non-stressed conditions. Conversely, crosses such as LM22 × LM81, LM95 × LM100, LM72 × LM44, LM22 × LM22, LM95 × LM02 and LM71 × LM44 recorded a grain yield of >5 t ha$^{-1}$ under terminal drought condition (Supplementary Table S3). The world average annual wheat yield is estimated at 3.2 t ha$^{-1}$ [23], which is below the grain yield values recorded for the selected genotypes. The crosses selected with a high grain yield under terminal drought show potential for further genetic advancement to increase grain yield in wheat. For instance, partial dominance was revealed in progeny LM72 × LM95, which recorded a higher grain yield than the mid-parent, but lower than the better-parent value under drought conditions across the tested environments (Supplementary Table S3), despite the non-significant SCA effect for this cross (i.e., LM72 × LM95) (Supplementary Table S5).

Regarding stomatal conductance, values between 31.93 and 74.18 mmol m$^{-2}$ s$^{-1}$ were recorded among the crosses under stressed field conditions (Supplementary Table S3). The moderate association between stomatal conductance with grain yield under drought-stress conditions (Table 5) suggests that selection for higher photosynthetic activity improves yield potential. Enhanced chlorophyll content under drought stress condition is important for improving yield response [24]. The low and positive association between chlorophyll content and grain yield under drought stress condition (Table 5) hinders the use of this physiological trait in the selection of segregating populations for yield improvement.

## 5. Conclusions

The present study assessed the combining-ability effects for agronomic and physiological traits among heat- and drought-tolerant bread wheat genotypes to select desirable parental genotypes and progenies for breeding. There were relatively weak associations between agronomic and physiological traits under drought-stress moisture regime. Parental genotypes LM72, LM81 and LM95 with desirable GCA effects for GY were selected for future crosses to develop high-yielding wheat genotypes for water-limited environments. Crosses such as LM71 × LM02, LM71 × LM81, LM82 × LM02, LM82 × LM81, LM22 × LM100, LM22 × LM81 and LM95 × LM22 were selected because they possess suitable SCA effects for GY. The selected parental genotypes and crosses were recommended for further crosses and genetic advancement to develop pure line cultivars.

## References

1. FAOSTAT. 2019. Available online: http:www.fao.org/faostat/en/#data/QC (accessed on 19 December 2019).
2. Labuschagne, M.; Moloi, J.; Van Biljon, A. Abiotic Stress Induced Changes in Protein Quality and Quantity of Two Bread Wheat Cultivars. *J. Cereal Sci.* **2016**, *69*, 259–263. [CrossRef]
3. Hernández-Espinosa, N.; Mondal, S.; Autrique, E.; Gonzalez-Santoyo, H.; Crossa, J.; Huerta-Espino, J.; Singh, R.P.; Guzmán, C. Milling, Processing and End-Use Quality Traits of CIMMYT Spring Bread Wheat Germplasm under Drought and Heat Stress. *Field Crops Res.* **2018**, *215*, 104–112. [CrossRef]
4. Beche, E.; Benin, G.; da Silva, C.L.; Munaro, L.B.; Marchese, J.A. Genetic Gain in Yield and Changes Associated with Physiological Traits in Brazilian Wheat During The 20th Century. *Eur. J. Agron.* **2014**, *61*, 49–59. [CrossRef]
5. Aisawi, K.; Reynolds, M.; Singh, R.; Foulkes, M. The Physiological Basis of The Genetic Progress in Yield Potential of CIMMYT Spring Wheat Cultivars from 1966 to 2009. *Crop Sci.* **2015**, *55*, 1749–1764. [CrossRef]
6. Lo Valvo, P.J.; Miralles, D.J.; Serrago, R.A. Genetic Progress in Argentine Bread Wheat Varieties Released between 1918 and 2011: Changes in Physiological and Numerical Yield Components. *Field Crops Res.* **2018**, *221*, 314–321. [CrossRef]
7. Mondal, S.; Singh, R.P.; Mason, E.R.; Huerta-Espino, J.; Autrique, E.; Joshi, A.K. Grain Yield, Adaptation and Progress in Breeding for Early-Maturing and Heat-Tolerant Wheat Lines in South Asia. *Field Crops Res.* **2016**, *192*, 78–85. [CrossRef] [PubMed]
8. Lopes, M.S.; Reynolds, M.P. Stay-Green in Spring Wheat Can Be Determined by Spectral Reflectance Measurements (Normalized Difference Vegetation Index) Independently from Phenology. *J. Exp. Bot.* **2012**, *63*, 3789–3798. [CrossRef]
9. Gao, F.; Ma, D.; Yin, G.; Rasheed, A.; Dong, Y.; Xiao, Y.; Xia, X.; Wu, X.; He, Z. Genetic Progress in Grain Yield and Physiological Traits in Chinese Wheat Cultivars of Southern Yellow and Huai Valley Since 1950. *Crop Sci.* **2017**, *57*, 760–773. [CrossRef]
10. El-Rawy, M.A.; Hassan, M.I.; Omran, M.F.; El-defrawy, M.M. Gene Action and Combining Ability of Cellular Thermotolerance in Bread Wheat (*Triticum aestivum* L.). *Plant Breed. Biotechnol.* **2018**, *6*, 206–220. [CrossRef]
11. Mwadzingeni, L.; Shimelis, H.; Tsilo, T.J. Combining Ability and Gene Action Controlling Yield and Yield Components in Bread Wheat (*Triticum aestivum* L.) under Drought-Stressed and Non-stressed Conditions. *Plant Breed.* **2018**, *137*, 502–513. [CrossRef]
12. Akhtar, N.; Waseem, A.; Mehmood, T.; Bano, S.; Raza, A.; Aziz, A. Gene Action Appraisal for Seed Yield and Related Traits in Bread Wheat. *J. Anim. Plant. Sci.* **2018**, *28*, 1457–1465.
13. Keser, M.; Gummadov, N.; Akin, B.; Belen, S.; Mert, Z.; Taner, S.; Topal, A.; Yazar, S.; Morgounov, A.; Sharmad, R.C. Genetic Gains in Wheat in Turkey: Winter Wheat for Dryland Conditions. *Crop J.* **2017**, *5*, 533–540. [CrossRef]
14. Chairi, F.; Vergara-Diaz, O.; Vatter, T.; Aparicio, N.; Nieto-Taladriz, M.T.; Kefauver, S.C.; Bort, J.; Serret, M.D.; Araus, J.L. Post-Green Revolution Genetic Advance in Durum Wheat: The Case of Spain. *Field Crops Res.* **2018**, *228*, 158–169. [CrossRef]
15. Sobhaninan, N.; Heidari, B.; Tahmasebi, S.; Dadkhodaie, A.; McIntyre, C.L. Response of Quantitative and Physiological Traits to Drought Stress in the Serim82/Babax Wheat Population. *Euphytica* **2019**, *215*, 32. [CrossRef]
16. Payne, R.W.; Murray, D.A.; Harding, S.A.; Baired, D.; Soultar, D. *Genstat Windows*, 17th ed.; VSN International: Hemel Hempstead, UK, 2017.
17. Rodríguez, F.; Alvarado, G.; Pacheco, Á.; Crossa, J.; Burgueño, J. AGD-R (Analysis of Genetic Designs with R for Windows) Version 5.0. International Maize and Wheat Improvement Center. 2018. Available online: http://hdl.handle.net/11529/10202 (accessed on 13 March 2019).
18. El-maghraby, M.A.; Moussa, M.E.; Hana, N.S.; Agrama, H.A. Combining Ability under Drought Stress Relative to SSR Diversity in Common Wheat. *Euphytica* **2005**, *141*, 301–308. [CrossRef]
19. Semehegn, Y.; Shimelis, H.; Laing, M.; Mathew, I. Combining Ability of Bread Wheat Genotypes for Yield and Yield-Related Traits under Drought-Stressed and Non-Stressed Conditions. *S. Afr. J. Plant. Soil* **2021**, *38*, 171–179. [CrossRef]
20. Shavrukov, Y.; Kurishbayev, A.S.; Jatayev, V.; Shvidchenko, L.; Zotova, F.; Koekemoer, D.; de Groot Soole, K.; Langridge, P. Early Flowering as a Drought Escape Mechanism in Plants: How Can It Aid Wheat Production? *Front. Plant Sci.* **2017**, *8*, 1950. [CrossRef]

21. Prieto, P.; Ochagavía, H.; Savin, R.; Griffiths, S.; Slafer, G.A. Physiological Determinants of Fertile Floret Survival in Wheat as Affected by Earliness per Se Genes under Field Conditions. *Eur. J. Agron.* **2018**, *99*, 206–213. [CrossRef]

22. Rebetzke, G.J.; Ellis, M.H.; Bonnett, D.G.; Mickelson, B.; Condon, A.G.; Richards, R.A. Height Reduction and Agronomic Performance for Selected Gibberellin-Responsive Dwarfing Genes in Bread Wheat (*Triticum aestivum* L.). *Field Crops Res.* **2012**, *26*, 87–96. [CrossRef]

23. Asseng, S.; Gaurin, J.R.; Raman, M.; Monje, O.; Kiss, G.; Despommier, D.D.; Meggers, F.M.; Gauthier, P.P.G. Wheat Yield Potential in Controlled-Environment Vertical Farms. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 19131–19135. [CrossRef]

24. Houshmandfar, A.; Rebetzke, G.J.; Lawes, R.; Tausz, M. Grain Yield Responsiveness to Water Supply in Near-Isogenic Reduced-Tillering Wheat Lines—An Engineered Crop Trait Near Its Upper Limit. *Eur. J. Agron.* **2019**, *102*, 33–38. [CrossRef]